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A review of Ichthyosauria from Portugal

Dissertação para obtenção do Grau de Mestre em Paleontologia

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Março, 2018

Acknowledgements

During the course of this thesis, several people have aided me performing my work to the best of my abilities, and I would like to thank them here for it.

To Professor Octávio Mateus, for agreeing to be my advisor, and for his continued assistance throughout all the stages of my work.

To Miguel Moreno Azanza, for his invaluable input and assistance in performing the phylogenetic analyses required of this work.

To Marco Marzola, for his assistance and patience in developing the specimen models used in this work.

To the Museu Geológico de Lisboa, and in particular Engineer Jorge Sequeira, for the access provided to the specimens of their collections, and the aid and patience as I observed them.

To the Museu Décio Tadeu, and in particular Professor Manuel Francisco, for the access provided to the specimens in their collections, and his quick availability, comprehension, and suggestions to improve my work.

To the Museu da Lourinhã, for the pleasant work environment that was provided to me during the writing of my thesis.

To my fellow colleagues Hugo Campos, André Saleiro, Filippo Maria Rotatori, Darío Estraviz and Alexandre Guillaume for their continued friendship throughout this period.

To Roschalle Machado, for providing me with comfortable living conditions during the course of my work.

And last but not least, to my parents, for always being there to aid me in my times of need and for always believing in me.

Resumo

O registo fóssil português de ictiossauros é composto por espécimes provenientes de S. Pedro de Moel, Alhadas, Cadima, Murtede, Casal Comba, Condeixa, Alvaiázere e Tomar, dentro da bacia Lusitaniana, com idades do Sinemuriano ao Aaleniano. Historicamente, Zbyszweski, Moitinho de Almeida e Veiga Ferreira identificaram os espécimes como pertencendo aos géneros *Ichthyosaurus* e *Stenopterygius,* e quando possível, às espécies *I. intermedius* e *S. uniter*. Contudo, mais de meio século passou desde que estas classificações foram feitas, e novos desenvolvimentos na filogenia e taxonomia dos ictiossauros tornaram-nas invalidas. Neste estudo, os espécimes foram revistos, e descrições mais completas foram realizadas, seguidas de uma análise filogenética com o objectivo de identificar os espécimes, mas o seu estado fragmentado, incompleto, e em alguns casos, mal preservado tornou os resultados da análise inconclusivos, e só um espécime, MDT-IST 85, foi classificado como pertencendo a uma espécie recentemente descrita, *I. larkini*. Mais estudos e novos desenvolvimentos na investigação deste grupo são necessários para uma classificação mais precisa dos espécimes portugueses.

Palavras-chave: *Ichthyosaurus, Stenopterygius, Jurássico, Bacia Lusitaniana, I. larkini*.

Abstract

The ichthyosaur fossil record of Portugal is composed of specimens from the localities of S. Pedro de Moel, Alhadas, Cadima, Murtede, Casal do Combo, Condeixa, Alvaiázere and Tomar, within the confines of the Lusitanian Basin, ranging in age from the Sinemurian to the Aalenian. Historical classifications by Zbyszewski, Moitinho de Almeida and Veiga Ferreira have identified the specimens as belonging to the genera *Ichthyosaurus* and *Stenopterygius*, and in the cases a species could be determined, *I. intermedius* and *S. uniter*. However, over half a century has passed since these specimens have first been document, and new developments in Ichthyosaur phylogeny and taxonomy have rendered these classifications invalid. In this study, we've reviewed the specimens and attempted to perform a more detailed description, after which a phylogenetic analysis was performed in order to identify the specimens, but the fragmented, incomplete, and in some cases poorly preserved stat of these has resulted in a largely inconclusive analysis, with only one specimen, 85, being unambiguously assigned to the recently described species *I. larkini*. Further studies and new developments in ichthyosaur research are required for a more accurate classification of the Portuguese specimens.

Keywords: *Ichthyosaurus, Stenopterygius, Jurassic, Lusitanian basin, I. larkini.*

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INTRODUCTION

History of discoveries

The Ichthyosauria are a group of Mesozoic reptiles, who stand out due to their extreme readaption to a marine environment, being strictly marine organisms, incapable of venturing on land (Sander, 2000). Being among the first groups of fossil reptiles recognized by science, the earliest records of this group date back to the eighteenth century, where fossils had been discovered by naturalists such as Johan Jakob Scheuchzer and Johan Jakob Baier, which resulted in much debate as to their origins, some considering the specimens to be remains of fish, while others considered them the remains of those who had perished in the biblical flood, in a time when geology was a poorly understood science, and fossils being proof of biblical events was common belief (Williston., 1914). For nearly a century afterwards, ichthyosaurs did not earn much attention, despite the abundance of specimens found in England and Germany, and only in 1814 did Sir Everard Home, a comparative anatomist, write about this group, which he described, illustrated and dubbed *Proteosaurus.* (Williston, 1914; Motani, 2005). Then, in 1821, that Karl D. Koenig would conduct a more detailed study, reaching the conclusion that these animals were an intermediate state between fish and reptile, and naming them *Ichthyosaurus*, the name by which the most recognized species of this group have been known since, and in the years after William Conybeare (Figure 1.1.1), Richard Owen, Georges Cuvier and others described and researched many specimens of ichthyosaurs, documenting most of the details on their skeletal structure, and finally, in 1835, Henri Marie de Blainville coined the name *Ichthyosauria*, the name by which this order of marine reptiles is now known. (Williston., 1914; Motani, 2005).

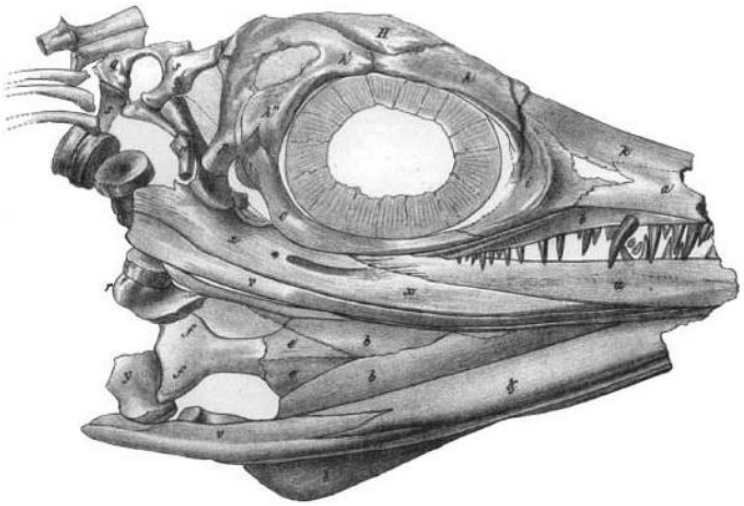

Figure 1.1.1: Skull of *Ichthyosaurus intermedius*, as figured by Conybeare in 1822, adapted from Massare *et al.*, 2017.

While there have been over two centuries of ichthyosaur related research, descriptions and new discoveries, of particular interest to us are the specimens found in the Portuguese fossil record. In this text, we intend to revisit the Portuguese Ichthyosaur fauna referenced in these works, and re-evaluate the specimens described, in order to verify the accuracy of these descriptions and determine a more thorough classification if necessary, while also briefly exposing what is known about this group.

Ecology

Ichthyosaurs are known for their readaptation to marine environments, which is comparable to that of cetacean mammals, and through these similarities, it can be inferred that they were fully marine animals, incapable of venturing on land, as their skeletal structure, with well-developed fins and thin, weakly joined vertebrae, would not be able to hold the animals' weight (Motani, 2005). This has resulted in a fully streamlined body shape, but there is a notable evolution. Earlier Triassic species show a more elongated body, with long tails, which indicates they resorted to anguilliform swimming, undulating the entire body like an eel. Later Triassic species had a more compact, laterally compressed body, with a small tail fin in the middle of the tail, which in later Jurassic and Cretaceous species developed into a large, semilunate fin on a narrow peduncle at the end of the tail, much like in sharks and tuna, which indicates a shift from anguilliform to thunniform swim-

ming, using only the side to side movements of the tail fin for locomotion. In all ichthyosaur species, the fins were used merely for steering and stabilizing, as seen in the figure below (Sander, 2000) (Figure 1.2.1).

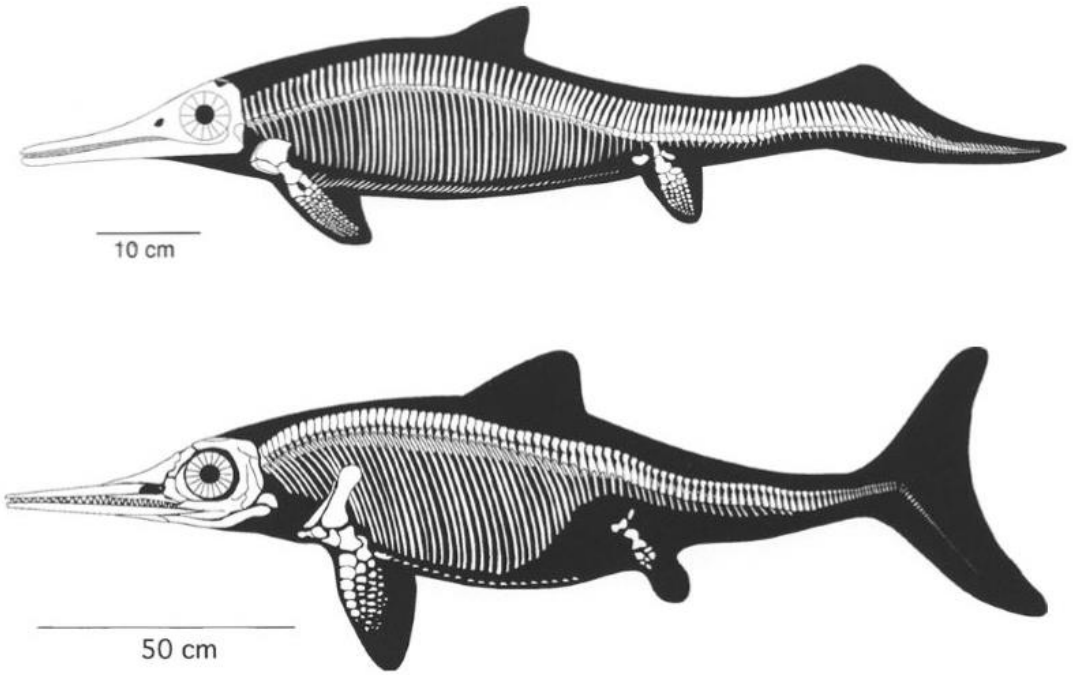

Figure 1.2.1: Body shape comparison of the Middle Triassic species *Mixosaurus*, more elongated and with a small tail fin, and the Lower Jurassic species *Stenopterygius*, more compact and with a fully developed tail fin, adapted from Sander, 2000.

The ichthyosaurs body shape, coupled with their long snout and teeth structure, indicates that ichthyosaurs were marine pursuit predators, using their large eyes to find prey in deep, dark waters. This has been confirmed by several specimens of ichthyosaur stomach contents, which contain thousands of cephalopod hooklets, indicating squids as their main prey item, as well as fish, smaller marine reptiles, including other ichthyosaurs, and in one documented finding, birds, suggesting they were also opportunistic feeders (Pollard, 1968; Kear *et al*, 2003). Earlier Triassic record also show an alternative durophagous diet in more primitive species, that would feed on hard shelled molluscs, using their shorter snouts and round teeth to crack shells. Due to their marine lifestyle, ichthyosaurs gave live birth to their young, as confirmed by several records of fossil specimens of pregnant females with embryos in different stages of development, usually in the posterior portion of the torso with their heads facing forward (Sander, 2000).

Osteology

The characteristic osteology of ichthyosaurs is the result of their terrestrial origins and readaptation to a marine environment, and it is also what makes identifying specimens of this group easy while also making finding homologies with other groups difficult. According to Sander, (2000), Ichthyosaur skulls generally sport a long snout, with a shorter snout variant that thins out at the tip, with round conical teeth, which is prevalent in larger species and indicates these fed on bigger prey items, such as large fish and smaller marine reptiles, and a longer snout variant that thins out closer to the eyes, with numerous slender isodont teeth, indicates a diet of fish and squid. The entire group sported large eyes, often protected by a sclerotic ring, which tend to influence the bone structure of the skull roof and the postorbital region, although the relative size of the eyes is smaller in larger species. The rostrum is composed of elongated premaxillary bones, and the nasals tend to elongate into the rostrum through the skull's midline, though this is variable depending on the species (Motani, 2005).

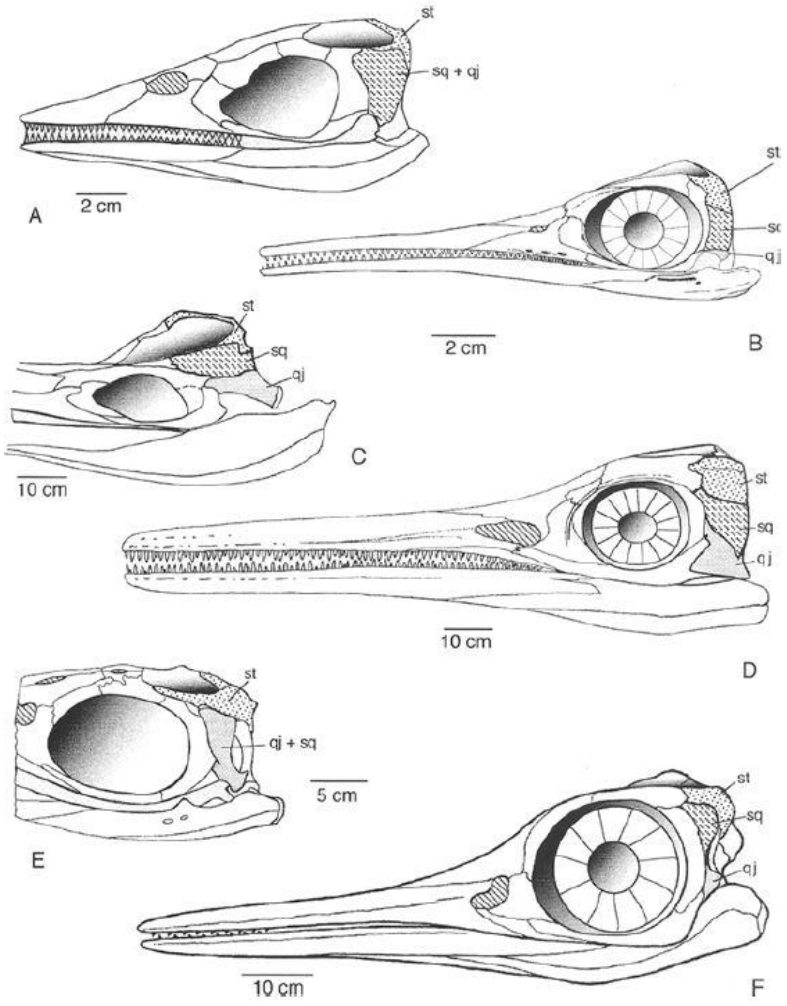

Figure 1.3.1: Skulls of *Grippia longirostris* (A), *Mixosaurus cornalianus* (B), *Cymbospondylus petrinus* (C), *Temnodontosaurus burgundiae* (D), *Ichthyosaurus* sp. (E) and *Ophthalmosaurus icenicus* (F), in left lateral view; st-Supratemporal, sq-Squamosal, qj-Quadratojugal; from Sander, 2000.

The roof of the ichthyosaur skull tends to vary, being broader with medium-sized upper temporal openings in earlier species, though it is normally constricted by the large eyes as mentioned above, and all ichthyosaurs lack postparietal and tabular bones at the back of skull roof. The cheek region is ossified and relatively large, but its structure and the number of bones comprising it have been source of much debate, mainly due to uncertainties regarding the bone of the posterolateral margin of the upper temporal opening. Generally, the cheek region will be composed of the supratemporal, squamosal and quadratojugal bones, though there are species where either the squamosal or the quadratojugal is not present (Figure 1.3.1). The occipital area has no outstanding characteristics, with the condyle being strongly convex in most ichthyosaurs, while the palate tends to be toothless and, in most species, is lacking the pterygoid flange (Sander, 2000). The lower jaw is generally as long as the rostrum, with a slender and deep posterior region which forms a retroarticular process past the jaw joint. The ichthyosaur lower jaw consists mainly of the dentary and the splenial which covers it anteriorly up to the symphysis (Maisch & Matzke, 2003). The teeth shape of ichthyosaurs varies depending on the diet, from the bulbous and button-like teeth of the durophagous species to the long, slightly recurved conical teeth of the piscivorous, to the large, conic, strongly edged teeth indicating a diet of larger prey, although an infolding of the dentine is an ichthyosaur synapomorphy, and tooth implantation of the subthecodont, ankylosed thecodont, thecodont and aulacodont types has been observed (Motani, 1997). Ichthyosaur vertebrae are short and lacking rib articulations on the side of the centra, which are generally higher than they are long, giving them their characteristic amphicoelous disk-like shape. The neural arches are simple structures, and the articular processes tend to be reduced structures at the base of the neural spine or completely absent in more advanced species. Because of the shortness and the small number of the vertebrae, Ichthyosaurs necks are short, with Jurassic and Cretaceous species usually having 40 to 50 presacral vertebrae, and one sacral vertebra that doesn't contact with the pelvic girdle in more developed species (Maisch & Matzke, 2000). Ichthyosaur vertebrae also lack transverse processes and the rib articulate partially with the centrum, and these articular facets can be distinguished in in six different patterns, which are very useful in species identification: double facets, single elongate facets, single round facets, double facets fusing into single round facets, single facets splitting into double facets, the point at which the split occurs also being important for identification. The rib heads, commonly sporting anterior and posterior grooves, are less diverse, and usually the double articular facets were attached to a single headed rib, although in

some Jurassic genus like *Ichthyosaurus* and *Stenopterygius*, double headed ribs were present. Articulated ichthyosaur specimens usually sport several thin gastralia, with an apparent ratio of 2 for each rib, although not enough specimens are well preserved enough to confirm this (Maisch & Matzke, 2000). The tail column is notable for having a variable morphology. Most Triassic species sported straight and long tails, with flattened vertebral centra and tall neural spines in anterior and middle areas of the tail column, which gave them the large lateral tail area necessary for their anguilliform swimming style. In later species, the tail grew shorter and developed a ventral flexure of variable angle, called the tailbend, which fossil discoveries with skin impressions have shown to form a semi-lunate shaped fin, which supports a thunniform swimming style (Sander, 2000.). The bone structure of the ichthyosaur shoulder girdle is not too different to the terrestrial condition, with a long and slender clavicle placed at the anterior margin, a large and triangular interclavicle in earlier species, and smaller and T-shaped in later ones. The scapula is no longer fused to the coracoid, and in earlier Triassic species it is T-shaped while in later post-Triassic dorsal blades rises from the ventral part, which contributes for the glenoid, and the coracoids are isometric bone plates which meet in a well-developed medial symphysis, with a variety of details of shape. Ichthyosaur limbs are composed of flattened and simplified bones with inflexible joints that form hydrodynamic, specialized fins. In the forefins, the humerus has a wide variety of shapes, being round and flattened, and possibly sporting and anterior notch, in Early and Mid-Triassic forms, while in later forms it sports thickened head, constricted shaft and a flattened, expanded distal end, while both the radius and ulna are generally shot and flat, possibly even wider than they are long, and depending on how they're integrated on the bone mosaic of the fin, may have a constricted shaft or be round. Also worth noting, is the high number of phalanges and a variable number of digits is observable, marking Ichthyosaur fins as the only non-pathological occurrence of polydactyly in amniotes (Maisch & Matzke, 2000; Motani, 2005). Primary digits are identified as the ones that contact the carpus region directly, while additional accessory digits are either result of the bifurcation of primary digits or inclusions on either margin of the fin, and alongside the bones, fins were stiffened by fibbers of connective tissue. Hindlimbs are smaller than the forelimbs, as much as half the length, but generally share the same anatomy, with the number of digits going from 6 to 3, depending on the degree of reduction, while the femur is a short, wide bone that can sport medial constriction. The pelvic girdle also shows a variable degree of reduction, the ischium, ilium and pubis have lost their sutural connection, the acetabulum is not ossified

in the center, and a thyroid fenestra between the posterior margin of the pubis and anterior margin of the ilium is observable in some species. While Triassic species tend to have wider, plate-like pubis and ischium, these bones are elongated and constricted in later species (Sander, 2000; Maisch & Matzke, 2000).

Systematics and phylogeny

Reptilia Laurenti, 1768
Ichthyopterygia Owen, 1840
Ichthyosauria de Blainville, 1835
Mixosauria Motani, 1999
Merriamosauria Motani, 1999
Shastasauria Motani, 1999
Euichthyosauria Motani, 1999
Parvipelvia Motani, 1999
Eurhinosauria Motani, 1999
Thunnosauria Motani, 1999
Ichthyosauridae Bonaparte, 1841
Ichthyosaurus De la Beche & Conybeare, 1821
I. intermedius Conybeare, 1822
Stenopterygiidae Woodward, 1932
Stenopterygius, Jaekel 1904
S. uniter, von Huene 1931

Despite the amount of time this group has been known to science, ichthyosaur phylogeny is still poorly understood, both in their relations with other groups, and amongst different ichthyosaurs. While their readaption to a marine environment has resulted in several autapomorphies that make ichthyosaur identification easy, it has also resulted in much convergent evolution, which has made it difficult to determine homologies with other groups. This, coupled with the fact that the earliest Triassic ichthyosaurs on record were already fully marine, extremely readapted animals, making any potential terrestrial ancestor that would allow for a connection unknown, leaves the position of ichthyosaurs within amniotes and their relations with other groups ambiguous (Maisch, 2010). This is also influenced by the fact that the fossil record is incomplete, and many of the more common

Jurassic specimens are in such excellent conditions that they can provide information about lifestyle and behaviour, which has encouraged many investigators to focus more on paleobiology than phylogeny (Sander, 2000.; Maisch, 2010). The earliest phylogenetic hypotheses focused mainly on characters of the anterior limbs from well-known post-Triassic specimens, dividing the Ichthyosaurs in two suborders, the Latipinnati, which had a normal or supernormal digits in the anterior limb, two of which originated from the intermedium of the proximal carpal row, and the Longipinnati, which had a subnormal number of digits, with only one contacting the distal surface of the intermedium, but this division was discovered in later studies by Mcgowan (1976), to not be well supported. Since then, many more inclusive analyses have been conducted, but a proper solution has yet to be reached. There is a general consensus that the Ichthyosauria might belong to a basal group of the Diapsida, and the most recent works on ichthyosaur phylogeny have determined Ichthyopterygia to be a monophyletic clade, with a sister relationship to Hupesuchia, but the exact phylogeny and origins of the ichthyosaurs remain to be determined (Figure 1.4.1) (Motani, 1999; Maisch, 2010; Moon, 2017).

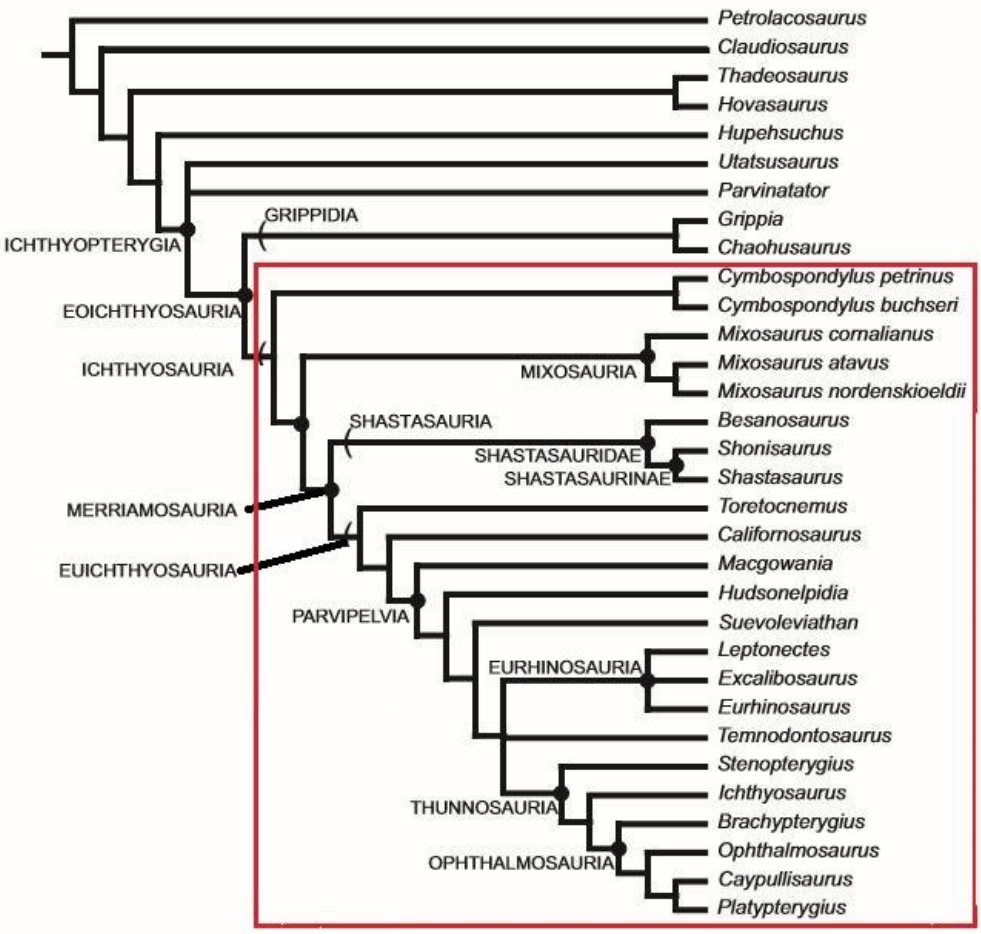

Figure 1.4.1: Phylogenetic relationships between Ichthyopterygia, with Ichthyosauria outlined, adapted from Motani., 1999.

Distribution

The Ichthyosaur fossil record ranges 145 million years, from the Olenekian (Early Triassic) to the Cenomanian (Late Cretaceous) (Motani, 2005). The earliest Triassic species were already fully marine animals, incapable of moving on land, and generally speaking, Ichthyosaur remains will be solely preserved in marine sediments, of the outer or inner continental shelf (Sander, 2000). Despite the considerable time span in which this group has lived, and the numerous specimens uncovered in excellent conditions, its fossil record is surprisingly incomplete and patchy, as fossil distribution is very uneven, and a majority of these specimens have been discovered in dig sites from Western Europe, mainly in Lower and Middle Jurassic faunas of England and Germany (Maisch, 2010) (Figure 1.5.1).

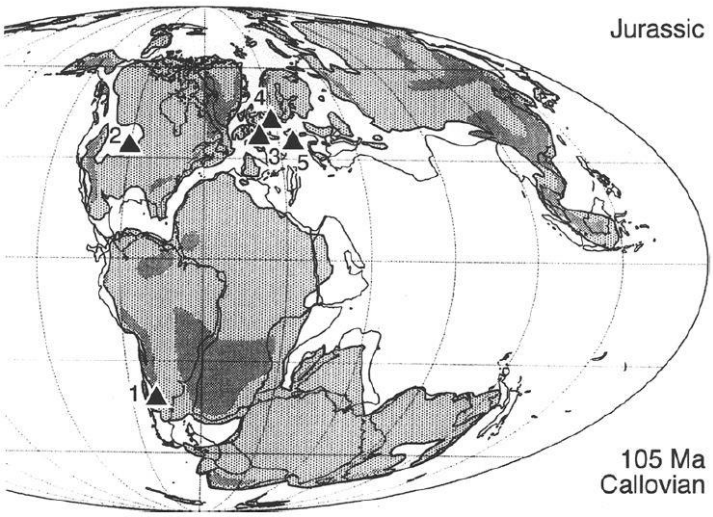

Figure 1.5.1: Main Ichthyosaur faunas of the Jurassic, nº 3,4 and 5 representing European dig sites, from Sander., 2000.

In Portugal, the Ichthyosaur fossil record ranges from the Sinemurian (Early Jurassic) to the Aalenian (Middle Jurassic). The specimens have been mostly identified as belonging to either the *Ichthyosaurus* or *Stenopterygius* genera, as will be expanded upon later.

Ichthyosaurs in Portuguese history

As far as we can tell, a majority of the documented ichthyosaur specimens in Portugal were found during stratigraphy fields works performed by the Sociedade de Serviços Geológicos de Portugal, but only in later years were they properly identified. The very first mentions of Portuguese ichthyosaurs were made by Paul Choffat, who in his works in 1885-1886, mentioned the presence of flattened vertebrae in the Pliensbachian formations in Pintanheira (Pentelheira), but it would not be until 1898 that Henri Sauvage would identify these, alongside a muzzle fragment found in the Toarcian formations of Alhadas, as *Ichthyosaurus sp.* (Figure 1.6.1), and associating them with the well-known ichthyosaur fauna of the English Lias (Sauvage, 1898).

Figure 1.6.1: First documented historical picture of the muzzle of *Ichthyosaurus sp*. from Alhadas, as identified by Henri Sauvage, adapted from Sauvage, 1898.

Later, in 1952, Georges Zbyszewski and Fernando Moitinho de Almeida would expand on this, by reviewing the collections of the Sociedade de Serviços Geológicos de Portugal. They identified maxillary fragments, an anterior right limb, and a collection of vertebrae from Praia de N. Senhora da Victória as the species *I. intermedius*, and maxillary and limb fragments and vertebrae from Pintanheira as *S. uniter*, while leaving maxillary fragments from Alhadas and Murtede and vertebrae from Cadima and Casal Comba (Casal do Combo) (Zbyszewski & Moitinho de Almeida, 1952) as Ichthyosaur Indet.. In 1958, Octávio da Veiga Ferreira would then further expand on this, documenting a newly discovered jaw fragment and vertebra from Praia da N. Senhora da Victória, and vertebrae from Condeixa (Figure 1.6.2) and Tomar as *S. uniter* and vertebrae occurrences from Praia da N. Senhora da Victória, Águas Madeiras (Águas de Madeiros), Casal Comba and Alvaiázere as *I. intermedius* (Veiga Ferreira, 1958).

Figure 1.6.2: Fossil dig of the vertebrae of Condeixa, from Veiga Ferreira, 1958.

The work of Veiga Ferreira, however, marked the beginning of a large hiatus in the investigation of Portuguese ichthyosaurs, and it would not be until 2007 that Rui Castanhinha and Octávio Mateus would review the marine reptiles of Portugal, revising and correcting previous classifications of the documented specimens (Castanhinha & Mateus, 2007). The current state of ichthyosaur knowledge in Portugal, based on these historical works, will be expanded on further on.

Geological and geographical context

All of the Ichthyosaur specimens of Portugal were found within the Lusitanian Basin, on the western central margin of the Iberian Peninsula. This is one of the Iberian sedimentary basins that developed during the Mesozoic, over the course of 135 M.a, due to distensive tectonic activity resulting from the fragmentation of the supercontinent Pangea and the opening and development of the Atlantic Ocean, conditioned by fault lines formed by late orogenic events from 300 to 280 M.a ago. Occupying an area of 20 000 Km^2, with a length of 200 Km in the NNW-SSE direction and 100 Km in the NEE-SWW direction, 2/3 of that area are in emerged continental territory, making it the only basin in the North Atlantic with a significant superficial area. During its evolution, the basin suffered four rifting episodes, in which the distensive tectonic activity intensified, and the lithostratigraphic units of the basin have been grouped by the episode they occurred in (Kullberg *et al.*, 2016.). Considering that the Portuguese Ichthyosaurs are from Sinemurian to the Aalenian rocks, we will address the units that formed within that time period, which formed during the first two rifting episodes (Figure 1.7.1).

The Coimbra formation, formed in the early Sinemurian during the first rifting episode, 199 M.A. ago, is a stratigraphic formation of limestones and dolomites, which can be divided in the base Coimbra Layers, composed of a cross-bedded dolomites and gray and red pelites, and the top S. Miguel Layers, composed of cross-bedded dolomitic limestones/limestones and gray marls (Duarte, 2002).

In the S. Pedro de Moel region, the Coimbra formation, with a thickness of over 100m, is particularly well represented, being noted for its rich fossiliferous contents, and there is a regional variation, between cross-bedded dolomitic limestones and gray marls in the northern Farol area, and gray marly limestones/marls in the southern Água de Madeiros region.

The Quiaios group, formed in a period from the Pliensbachien to the Aalenian, is comprised of three main formations:
- At the base, the Vale das Fontes Formation, with a variable thickness (30±10m in Alvaiázere and 73±6m in Águas de Madeiros), composed mainly of blackened lumpy marls and marly limestones (Duarte, 2007.)

- The Lemede Formation composed mainly of thick limestones, although there is regional variation (6±3 m in Alvaiázere) (Duarte, 2007).

- At the top, the S. Gião Formation, composed of limestones and marls, arranged in a laminated cross-bedded pattern, which shows regional variation (100m in Alvaiázere and over 40m in Água de Madeiros), and is also indicative of tempestitic-turbiditic activity. The top and bottom limits of this formation are marked by the Speciosum and Polymorphum biozones respectively. (Kullberg *et al.*, 2016.)

Most of these lithostratigraphic units are noted for being rich in fossils of marine species, with a strong presence of ammonites, brachiopods, lamellibranches, and ostracods, which, coupled with the carbonate composition of the majority of their sediments, suggests the depositions of these formations occurred in a marine environment. More specifically, the observable disappearance of dolomitic facies and increase in fossil presence in the Coimbra Formation suggest a steadily increasing sea level, and the alternating limestone and marl sediments suggest the occurrence of various transgressive

cycles, the peak of which will coincide with the more marly, fossil rich units. (Duarte *et al.*, 2014.)

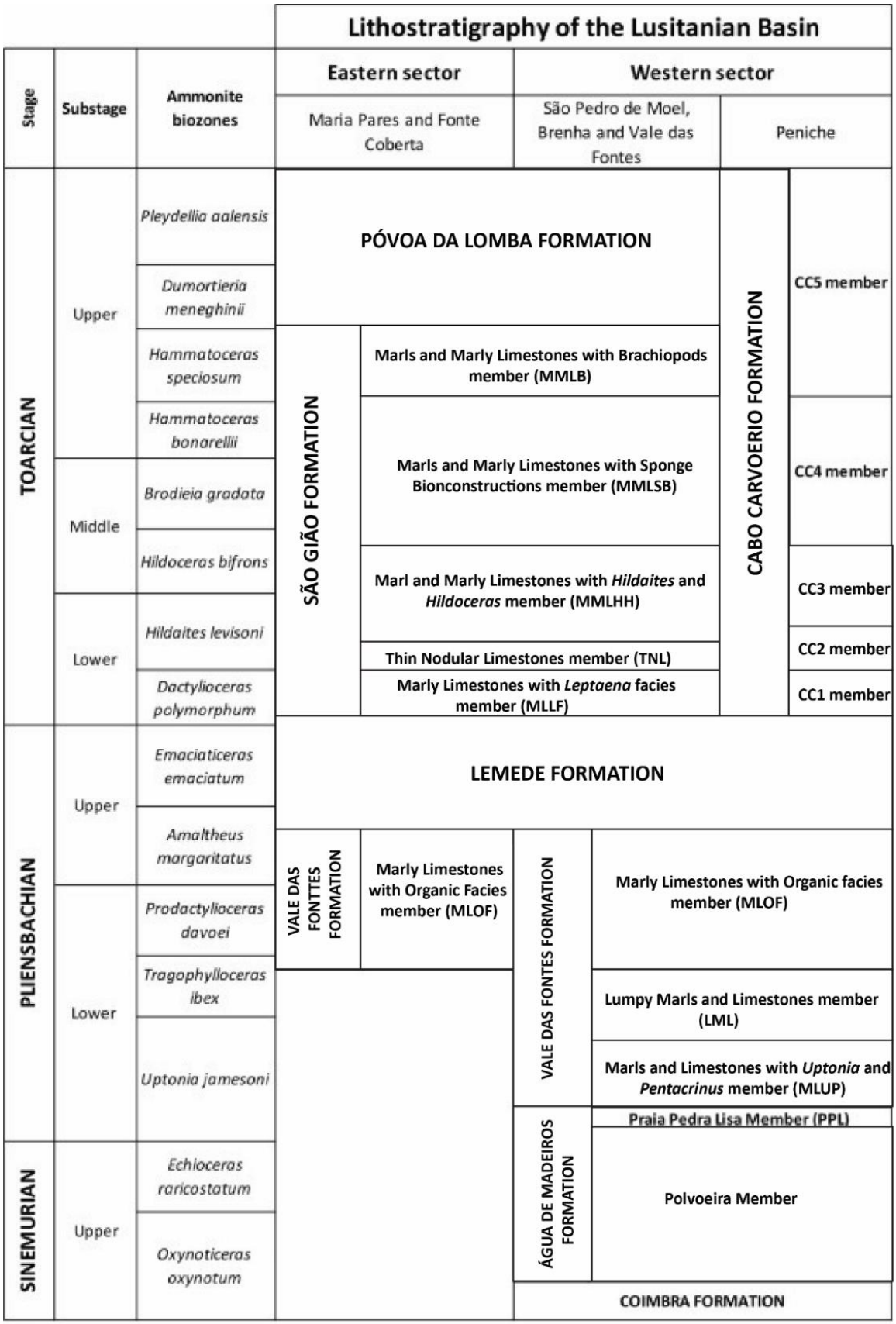

Figure 1.7.1: Lithostratigraphy of the Lower Jurassic (Upper Sinemurian to Upper Toarcian) of the Lusitanian basin, adapted from Correia *et al*, 2018.

SPECIMENS BY LOCALITY

Table 1: Table representing the Portuguese ichthyosaur specimens' distribution by locality.

Localities	Sinemurian	Pliensbachian	Toarcian	Aalenian	Uncertain age
S. Pedro de Moel	MG 4745				
Praia de Nossa Senhora da Vitória	104 85 103	MG 4749			
Pintanheira		MG 4751 MG 4747 MG 4755			
Águas de Madeiros	MG 4748				
Alhadas				MG 36	
Cadima					MG 4752
Murtede					MG 35
Casal do Combo					MG 4746
Condeixa			MG 25182 MG 25183		
Alvaiázere		MG 25184			
Tomar				MG 4743 MG 4753	
Unknown locality					MG 25186

Municipality of Marinha Grande

S. Pedro de Moel (39°45'28.25"N, 9° 1'47.24"W)

Sinemurian:

- MG 4745: An undocumented vertebra, identified as *I. intermedius,* found north of S. Pedro de Moel.

Municipality of Alcobaça

Águas de Madeiros (39°44'6.81"N, 9° 2'8.11"W)

Sinemurian:

- MG 4748: A set of 2 vertebrae, identified as *I. intermedius,* documented by Ferreira in 1958.

Praia de N. Senhora da Victória (39°42'6.90"N, 9° 2'53.55"W)

Sinemurian:

- MDT-IST 104: Maxillary fragments with teeth, identified as *I. intermedius,* documented by Zbyszewski in 1952.

- MDT-IST 85: An almost complete anterior right limb, identified as *I. intermedius,* documented by Zbyszewski in 1952.
- MDT-IST 103: A set of fragmented vertebrae, identified as *I. intermedius,* documented by Zbyszewski in 1952.

Pliensbachian:

- MG 4749: A jaw fragment, sporting 46 teeth, identified as *S. uniter* documented by Ferreira in 1958.

Pintanheira (39°43'37.01"N, 9° 2'31.72"W)

Pliensbachian:

- MG 4751: Two jaw fragments, identified as *S. uniter*, documented by Zbyszewski in 1952.
- MG 4747: Fin fragments (radius, digits, femur), identified as *S. uniter*, documented by Zbyszewski in 1952.
- MG 4755: A set of 38 vertebrae, identified as *S. uniter*, documented by Zbyszewski in 1952.

Municipality of Alvaiázere

Alvaiázere (39°49'25.48"N, 8°22'50.62"W)

Pliensbachian:

- MG 25184: A single, poorly preserved vertebra, identified as *I. intermedius,* documented by Ferreira in 1958.

Municipality of Condeixa-a-nova

Condeixa (40° 6'44.88"N, 8°30'0.21"W)

Toarcian:

- MG 25182: A set of 15 vertebrae, identified as *Stenopterygius sp.*, documented by Ferreira in 1958.
- MG 25183: A set of 13 vertebrae, identified as *Stenopterygius sp.*, documented by Ferreira in 1958.

Municipality of Figueira da Foz

Alhadas (40°11'8.11"N, 8°47'29.86"W)

Aalenian:

- MG 36: A jaw fragment, identified as *S. uniter*, documented by Sauvage in 1898.

Municipality of Torres Novas

Tomar (39°30'36.11"N, 8°29'2.29"W)

Aalenian:

- MG 4743: A dorsal vertebra, identified as *S. uniter*, documented by Ferreira in 1958.
- MG 4753: A caudal vertebra, identified as *Stenopterygius*, documented by Ferreira in 1958.

Municipality of Mealhada

Casal Comba (40°22'4.21"N, 8°28'0.28"W)

Uncertain age:

- MG 4746: Two caudal vertebrae, identified as *I. intermedius*, documented by Ferreira in 1958.

Municipality of Cantanhede

Murtede (40°21'37.05"N, 8°30'18.78"W)

Uncertain age:

- MG 35: Maxillary fragments, unidentified, documented by Castanhinha and Mateus in 2007.

Cadima (40°19'32.58"N, 8°38'26.58"W)

Uncertain age:

- MG 4752: Set of 3 articulated vertebrae, identified as *Ichthyosaurus sp.*, documented by Castanhinha and Mateus in 2007.

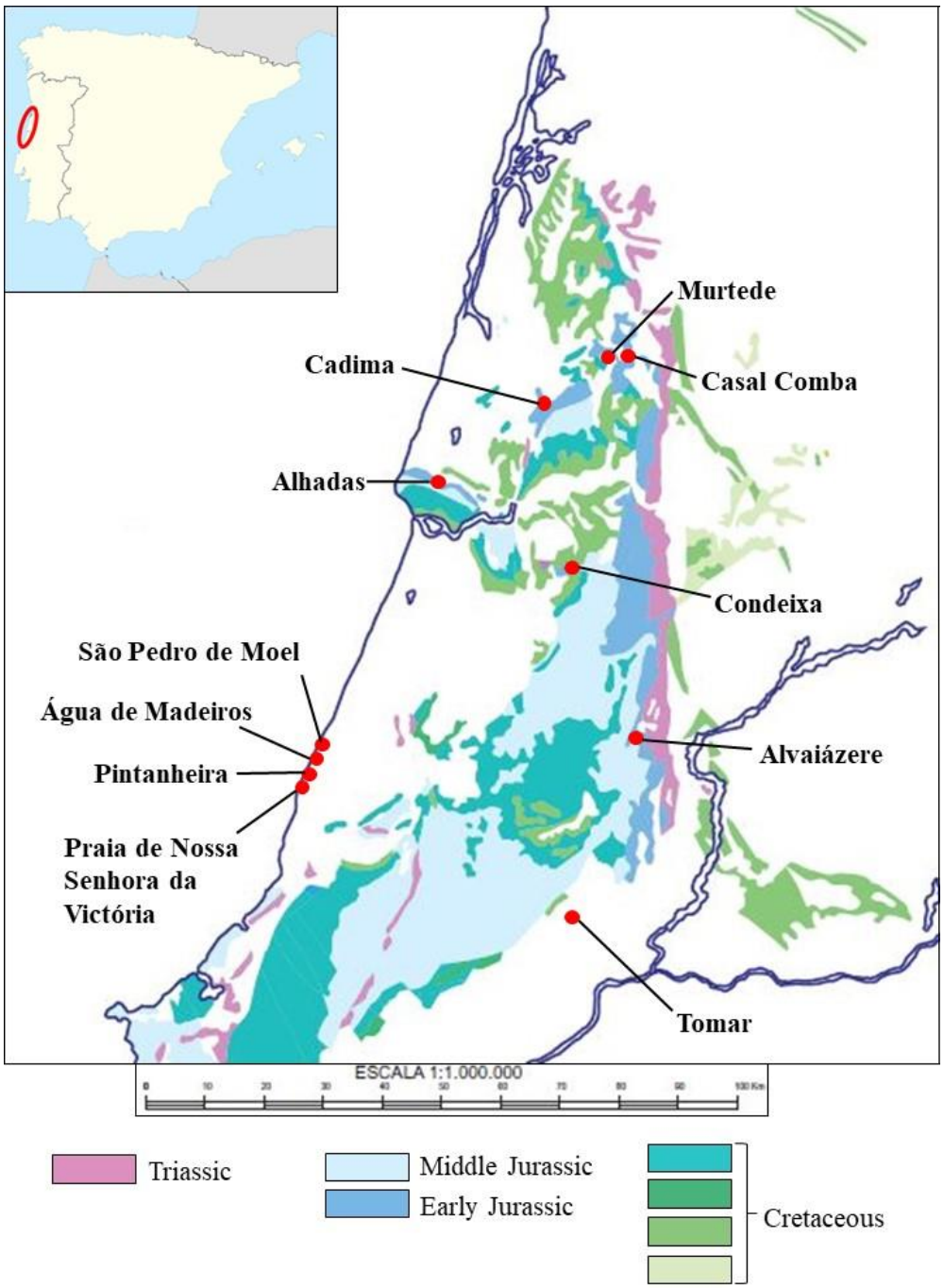

Figure 2.1: The documented localities where Ichthyosaur fossils have been uncovered, within the Lusitanian basin.

METHODOLOGY

During the course of this thesis, research was performed to determine the historical information regarding the observed ichthyosaur specimens, seeking to discover who first referenced them, where were they discovered, how were they described, and what age did they belong to. After which, an attempt was made at a more accurate description of the specimens, based on the characters described by Moon, (2017) (See Appendix I and II), with the creation of 3D models in order to facilitate character observation (see Appendix III), although the very fragmentary nature of the specimens made character identification difficult. And lastly, a phylogenetic analysis was performed. The specimens were coded and based on the matrix provided by the work of Benjamin C. Moon, 2017(Consistency indices for strict consensus and 50% majority rule trees=0.150 and 0.175; retention indices=0.521 and 0.601), and a maximum parsimony analysis was performed. Due to their incomplete state, each specimen was analysed individually, resulting in 105 operational taxonomic units used by analysis, using TnT version 1.5 (Goloboff & Catalano, 2016), with the intent of more accurately discerning the specimens' affinities to ichthyosaur taxa.

ICHTHYOSAUR SPECIMENS OF PORTUGAL

SINEMURIAN

MDT-IST 104

Historical information

Referenced by: Zbyszewski *et al*, 1952.

Classified as: *Ichthyosaurus intermedius.*

Locality: Praia de Nossa Senhora da Victória, S. Pedro de Moel.

Age: Sinemurian (199.3-190.3 M.a).

Formation: Possibly Coimbra Formation.

Elements: Fragments of the upper and lower jaw with a number of teeth, some of them broken, with tapered, pointy subcircular tips, with thin streaks and grooves, slightly swollen roots, and a smoother area at the base of the crown (Figure 3.1.1) (Zbyszewski *et al*, 1952).

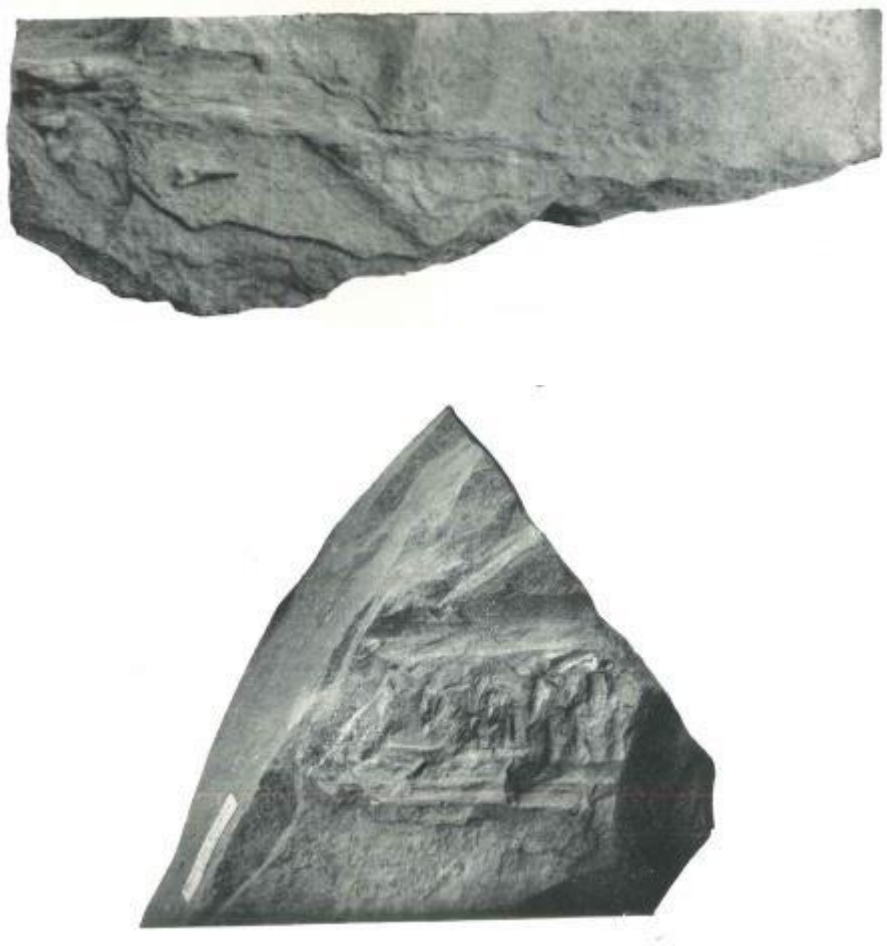

Figure 3.1.1: First documented historical picture of MDT-IST 104, identified as maxillary fragments of *Ichthyosaurus intermedius*, after Zbyszewski *et al.*, 1952.

New description

The specimen is composed of 2 blocks, each containing bone fragments of the upper and lower jaw. Six well-developed teeth are observable, apparently distributed in a single row with no bony fixation to the jaw. The teeth are round, and the enamel is ornamented with prominent grooves with a poorly defined base, while the roots show subtle striations.

Phylogenetic analysis

Specimen MDT-IST 104 yielded 22124 most parsimonious trees (MPTs), each with a length of 1666 steps. The strict consensus is poorly resolved, placing the specimen simultaneously in the species *Ichthyosaurus larkini*, and at the base of the Ophthalmosauridae node (Figure 3.1.2).

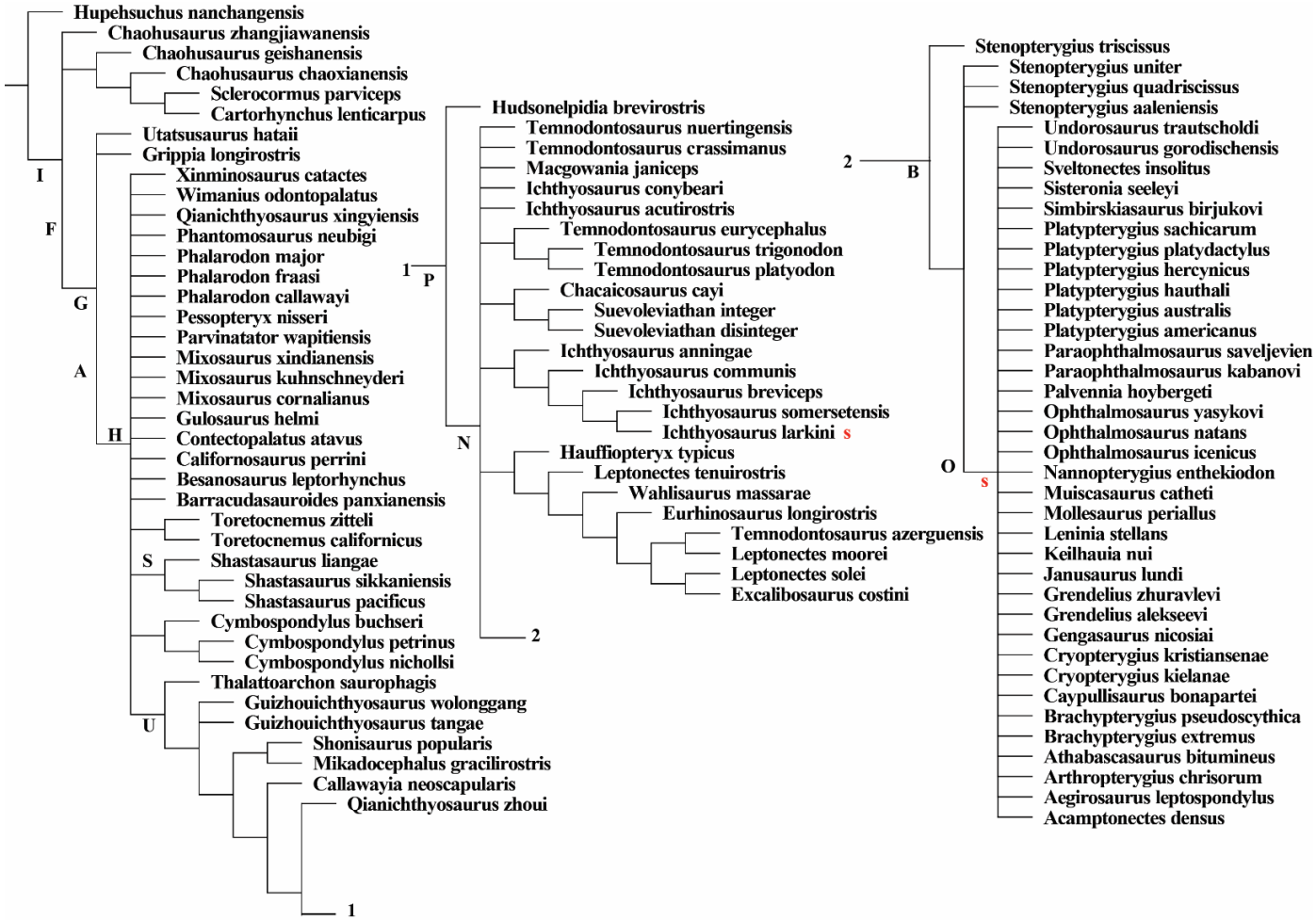

Figure 3.1.2: Strict consensus tree for specimen MDT-IST 104, result of 22124 MPTs, 1666 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MDT-IST 85

Historical information

Referenced by: Zbyszewski *et al*, 1952.

Classified as: *Ichthyosaurus intermedius.*

Locality: Praia de Nossa Senhora da Victória, S. Pedro de Moel.

Age: Sinemurian (199.3-190.3 M.a).

Formation: Possibly Coimbra Formation.

Elements: An almost complete anterior right limb, composed of a humerus articulated with a large radius and damaged ulna on the ventral surface, with five articulated digits composed of small flat bones, and two rows of marginal ossicles, corresponding to a radial digit (Figure 3.2.1) (Zbyszewski *et al*, 1952).

Observations: The damage sustained by the specimen seems to have been done by a sharp instrument. Next to the specimen, a group of disassembled ossicles were found, thought to have belonged to the individual's left fin.

Figure 3.2.1: First documented historical picture of MDT-IST 85, identified as an anterior right limb of *I. intermedius*, after Zbyszewski *et al.*, 1952.

New description

The specimen is composed of a complete, anterior right fin. The humerus, slightly proximodistally longer than anteroposteriorly wide, and in dorsal view, equally as wide proximally and distally, lacks a differentiated proximal head, and the anterior margin is markedly concave, while a proximally reduced anterior flange is present. The dorsal trochanter is well-developed but a protruding deltopectoral crest and a plate-like dorsal ridge are absent. The distal facets are terminally placed, approximately equal in size, apparently continuous, and the ulnar facet does not deflect posterodistally. The anterodistal extremity shows no tuberosity, and no antero or postero distal facets for the sesamoid. There is no contact between the humerus and the intermedium. The epipodial and metapodial elements are flattened and plate-like, with no notching on the anterior and posterior edges of the fin, and one postaxial accessory digit is observable. The radius and the ulna are equal in size, lacking an interosseous space between them, and the radius is wider than long. The ulna is severely damaged and difficult to discern, but is apparently

equally wide anteriorly and posteriorly, and the posterior margin is convex, and as thick as the rest of the ulna. The manual pisiform is absent. The intermedium, damaged like the ulna, is smaller than the ulnare, located between the radius and the ulna, and apparently as wide as it is long, with a pointed proximal shape, an angular distal edge, and 2 directly supported digits. The ulnare sports one distal facet, supporting a single digit. There are 5 observable carpals, although 2 of those are likely accessory elements, and all of them are of comparable size. There are 4 observable ossified elements in the metacarpal row, and a preaxial accessory digit is absent. The manual metacarpals I is absent, while II-IV are rounded in shape. The manual phalanges are numerous, tightly packed polygons proximally and rounded distally, and a digital bifurcation is observable.

Phylogenetic analysis

Specimen MDT-IST 85 yielded 11484 MPTs, each with a length of 1674 steps. The strict consensus is well resolved, placing the specimen in the species *I. larkini* (Figure 3.2.2).

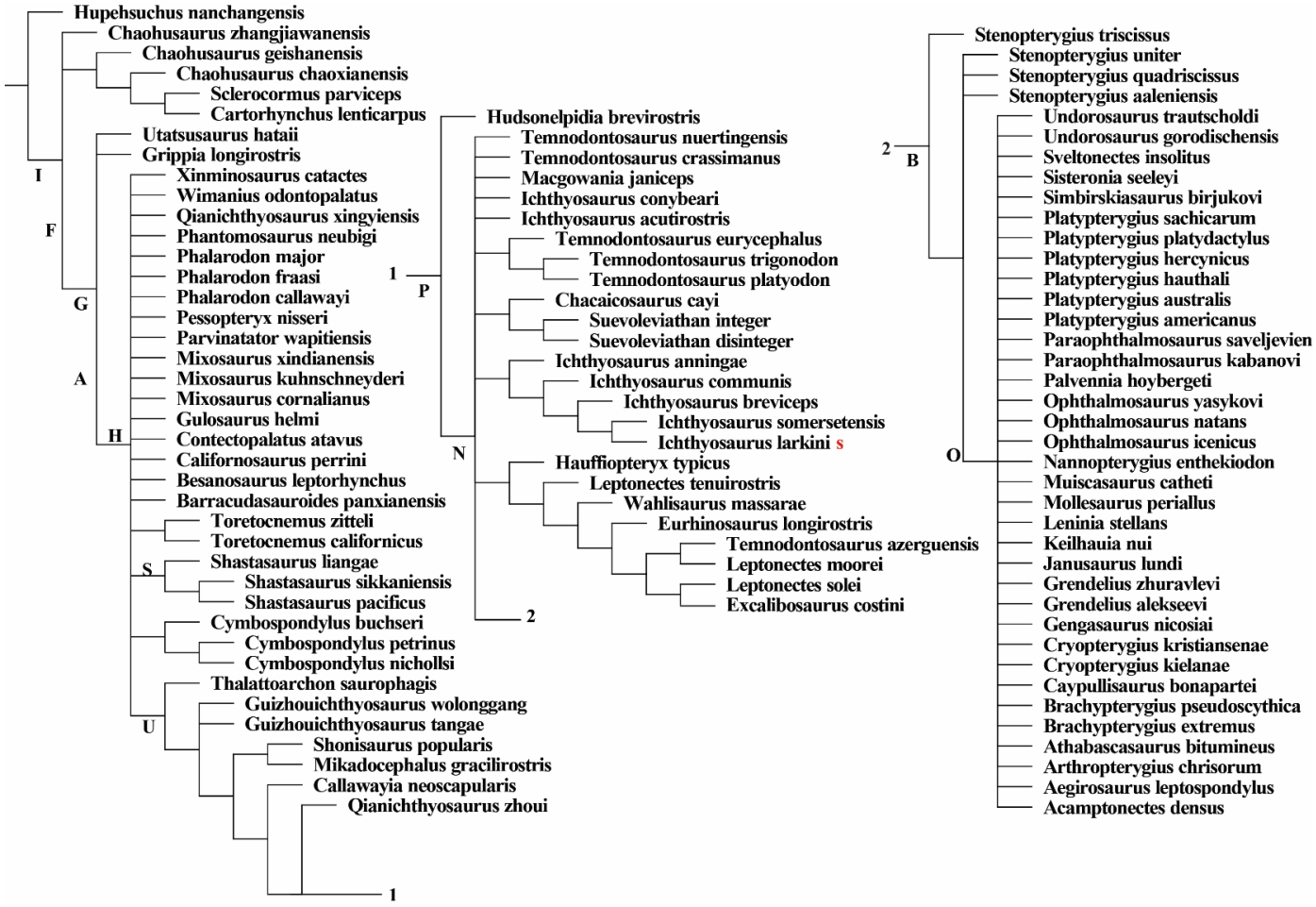

Figure 3.2.2: Strict consensus tree for specimen MDT-IST 85, result of 11484 MPTs, 1674 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MDT-IST 103

Historical information

Referenced by: Zbyszewski *et al*, 1952.

Classified as: *Ichthyosaurus intermedius.*

Locality: Praia de Nossa Senhora da Victória, S. Pedro de Moel.

Age: Sinemurian (199.3-190.3 M.a).

Formation: Possibly Coimbra Formation.

Elements: A set of several vertebrae and fragments of vertebrae, belonging to the same animal, embedded in very hard grey limestone. The three most complete ones have heights of 15-16mm, widths of 16,5-17, and a distance between concavities of 21mm (Figure 3.3.1) (Zbyszewski *et al*, 1952).

Figure 3.3.1: First document historical picture of one of the vertebra-bearing blocks of MDT-IST 103, identified as vertebrae of *I. intermedius*, after Zbyszewski et al., 1952.

New description

The specimen is composed of over ten vertebrae and rib fragments embedded in grey limestone. With the 3 most complete one observable being 15-16mm in height, and 16,5-17mm in width, their outline is less than 3,5 times as high as it is long. The specimen is otherwise to fragmented for other details to be discernible.

Phylogenetic analysis

Specimen MDT-IST 103 yielded 50000 MPTs (overflow occurred), each with a length of 1666 steps. The strict consensus is very poorly resolved, placing the specimen in 38 locations in the phylogenetic tree (Figure 3.3.2).

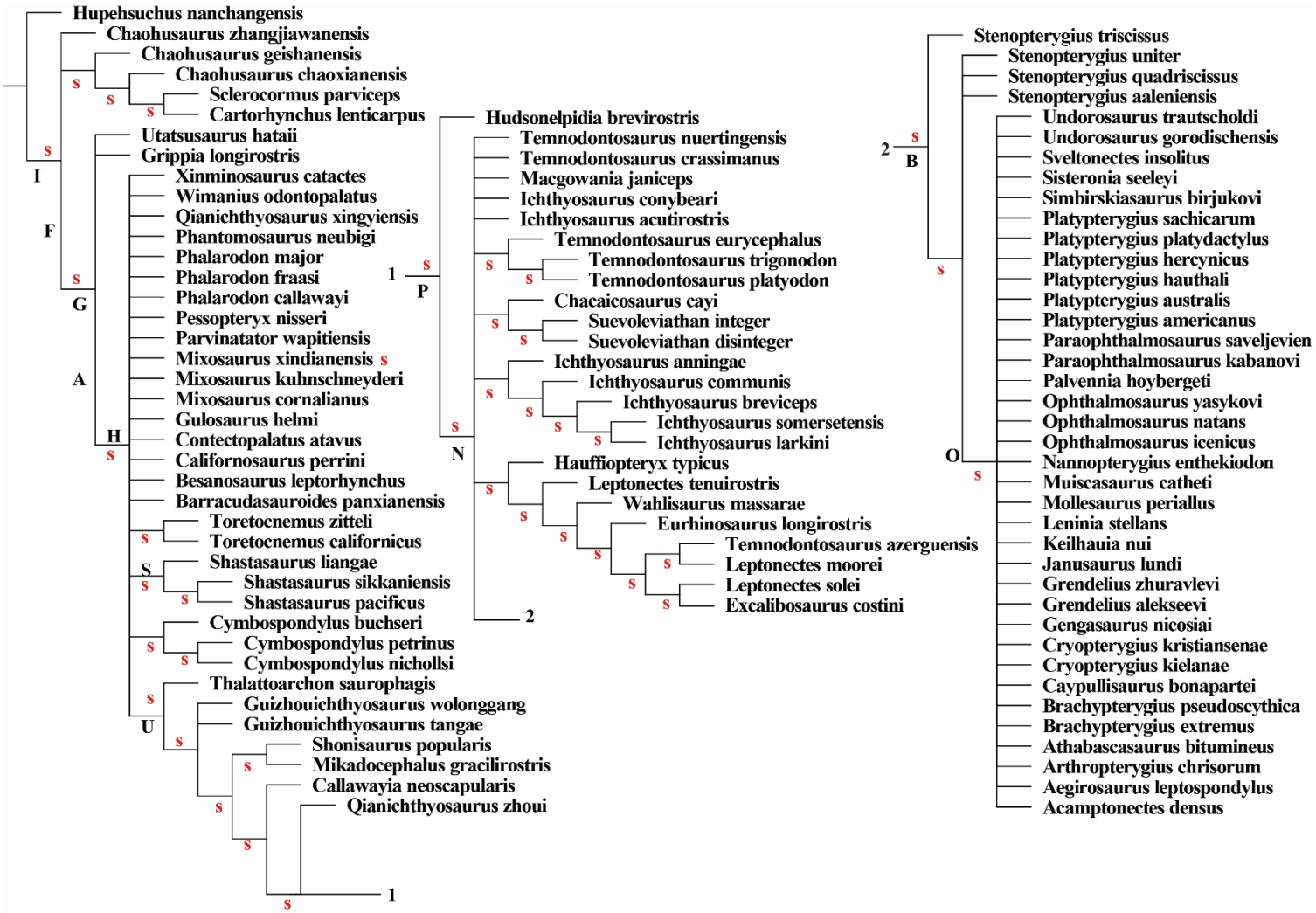

Figure 3.3.2: Strict consensus tree for specimen MDT-IST 103, result of 50000 MPTs, 1666 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MG 4745

Historical information

Referenced by: Undocumented.

Classified as: *Ichthyosaurus intermedius.*

Locality: S. Pedro de Moel.

Age: Sinemurian (199.3-190.3 M.a).

Formation: Undetermined.

Elements: A single vertebra with a diameter of 12x13mm and a width of 8mm.

Observations: It is noted to have been found 3m above a layer of *Asteroceras.*

New description

The specimen is composed of a single vertebra, 12x13mm in diameter and 8mm in width, and comparison with other specimens suggests it is a caudal vertebra. It is short, strongly laterally compressed, and the indentations present suggest a vertical neural spine, although this is not visible.

Phylogenetic analysis

Specimen MG 4745 yielded 50000 MPTs, each with a length of 1666 steps. The strict consensus is poorly resolved, placing the specimen simultaneously in the species *Eurhinosaurus longirostris*, in a basal position between the *Stenopterygius* clade and the Ophthalmosauridae node, as well as at the base of this last one (Figure 3.4.1).

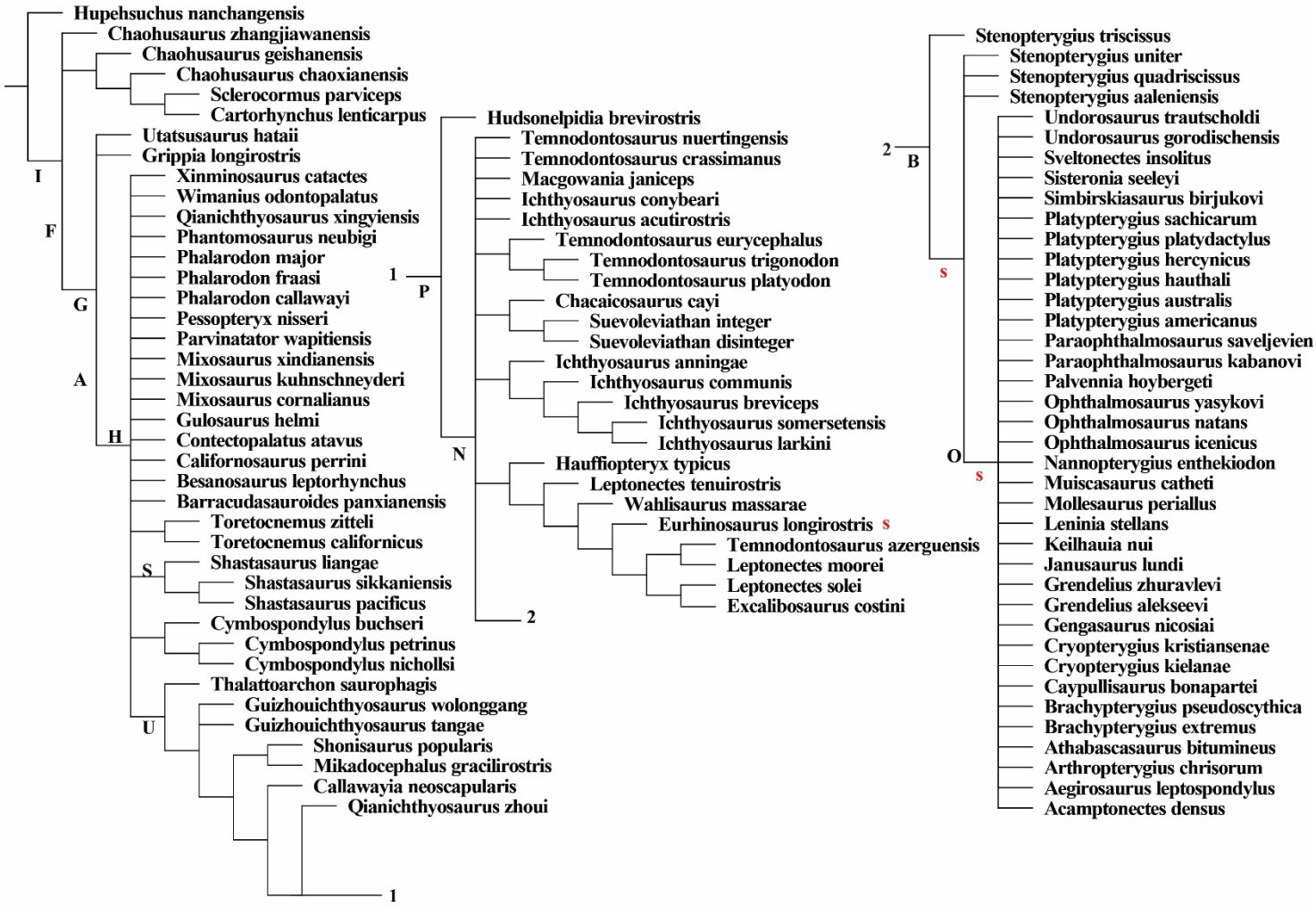

Figure 3.4.1: Strict consensus tree for specimen MG 4745, result of 50000 MPTs, 1666 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

PLIENSBACHIAN

MG 4749

Historical information

Referenced by: Veiga Ferreira. 1958.

Classified as: *Stenopterygius uniter*.

Locality: Praia de Nossa Senhora da Victória, S. Pedro de Moel.

Age: Pliensbachian (190.8-182.7 M.a).

Formation: Possibly Vale das Fontes Formation.

Elements: Two maxillary fragments, with 46 teeth, 26 in the upper and 20 in the lower maxilla. In the upper maxilla both nasal bones are observable, as well as part of the nasal fossa and pieces of the lacrimal bone, while the lower maxilla has no bones other than the maxillary (Figure 3.5.1) (Veiga Ferreira, 1958).

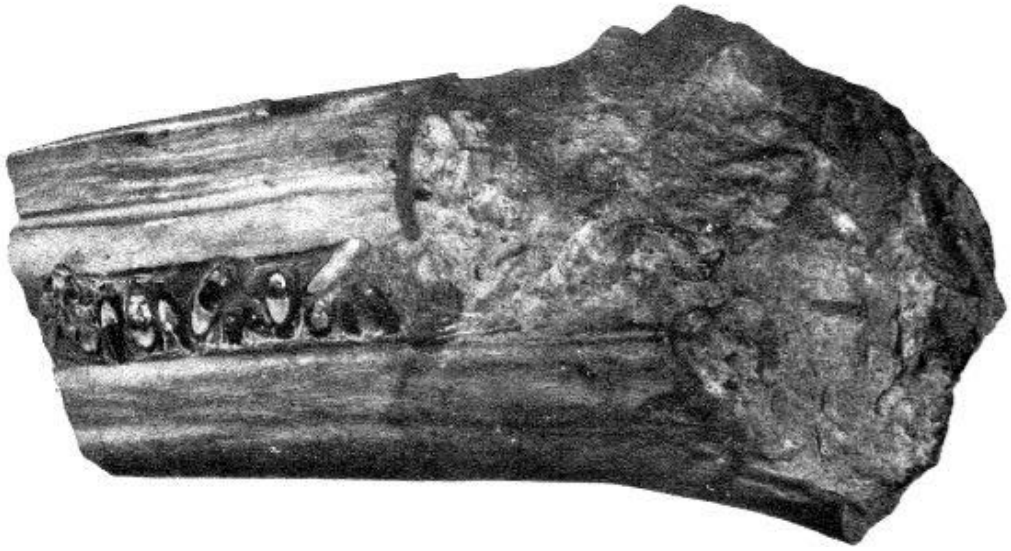

Figure 3.5.1: First documented historical picture of MG 4749, identified as maxillary fragments of *S. uniter*, after Veiga Ferreira., 1958.

New description

The specimen is composed of a snout fragment, 50±5mm in height distally, 75±mm proximally. The upper jaw is 144±5mm in length, 40±5mm in width distally, 60±5mm proximally. The lower jaw is 127±5mm in length, 32±5mm in width distally, 44±5mm proximally, and tooth length ranges from 4±5mm to 20±5mm. The premaxilla bears both a supranarial and subnarial process, and there is a contact with what is interpreted to be the distal edge of the nasal. The maxilla is tooth bearing, but little else is discernible. The lower jaw is well developed, smaller but not slenderer that the upper jaw, with a ventral margin apparently slightly concave in lateral view, while the dentary is lacking a labial shelf. 2 symmetric elements are observable ventrally, interpreted to be the splenial bone. The dentition is appears well-developed, with an aulacodont implantation (Teeth set on groove, not ankylosed (Motani, 1997)) but seem to lack a bony fixation or Plicidentine (Transversely sinuous dentine (Motani, 1999)). There's a single tooth row, and both and upper and lower dental grooves appear to be present. Palatine and pterygoidal teeth are absent. Tooth replacement appears to be regular, with the replacement tooth apparently inside the pulp cavity if the predecessor. The tooth enamel layer is ornamented with prominent ridges and grooves, and its base is well defined and precise, while subtle

striations are observable on the roots. The teeth are round, with a conical crown (Figure 3.5.2).

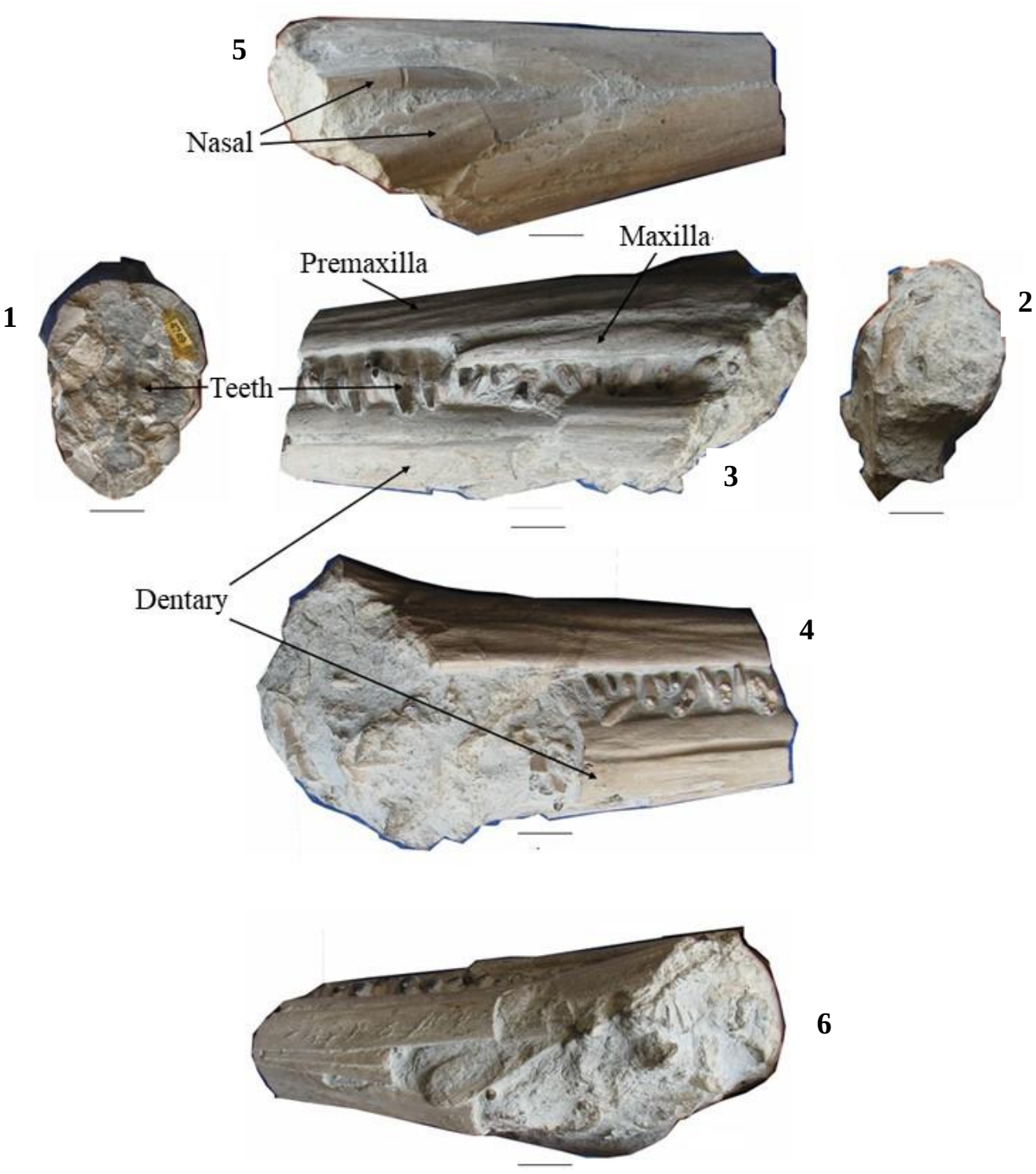

Figure 3.5.2: MG 4749 (Pictures by Octávio Mateus), composed of tooth-bearing maxillary fragments. 1-Anterior view; 2-Posterior view; 3- Left view; 4-Right view; 5-Dorsal view; 6-Ventral view. Bar marks 2 cm.

Phylogenetic analysis

Specimen MG 4749 yielded 21952 MPTs, each with a length of 1670 steps. The strict consensus, like specimen 104's, is poorly resolved, placing MG 4749 simultaneously as *I. larkini* and at the base of the Ophthalmosauridae node (Figure 3.5.3).

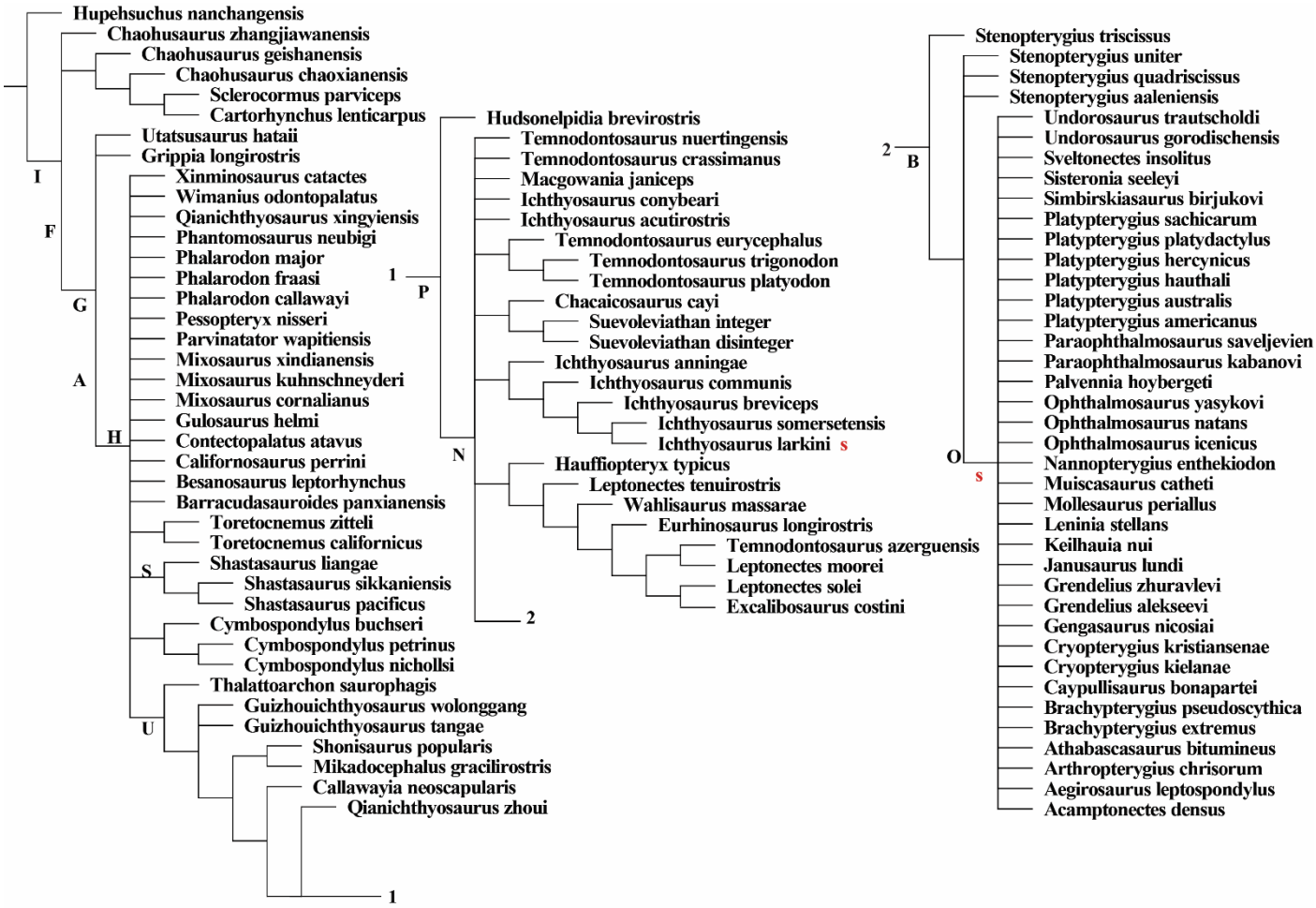

Figure 3.5.3: Strict consensus tree for specimen MG 4749, result of 21952 MPTs, 1670 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MG 4747

Historical information

Referenced by: Zbyszewski *et al*, 1952.

Classified as: *Stenopterygius uniter*.

Locality: Pintanheira, S. Pedro de Moel.

Age: Pliensbachian (190.8-182.7 M.a).

Formation: Possibly Lemede Formation.

Elements: A radius with a strongly anchored anterior edge, with a height of 56mm and a length of 60mm; an incomplete fin of nine ossicles organized in two rows, 140mm in length and 54mm in width; an isolated ossicle of the same kind; tip of a right femur, 68 mm in length, 61mm in width (Figure 3.6.1) (Zbyszewski *et al*, 1952).

Observation: There was some noted uncertainty as to whether the radius belonged to *Stenopterygius* or *Leptopterygius,* though it was ultimately classified as the former.

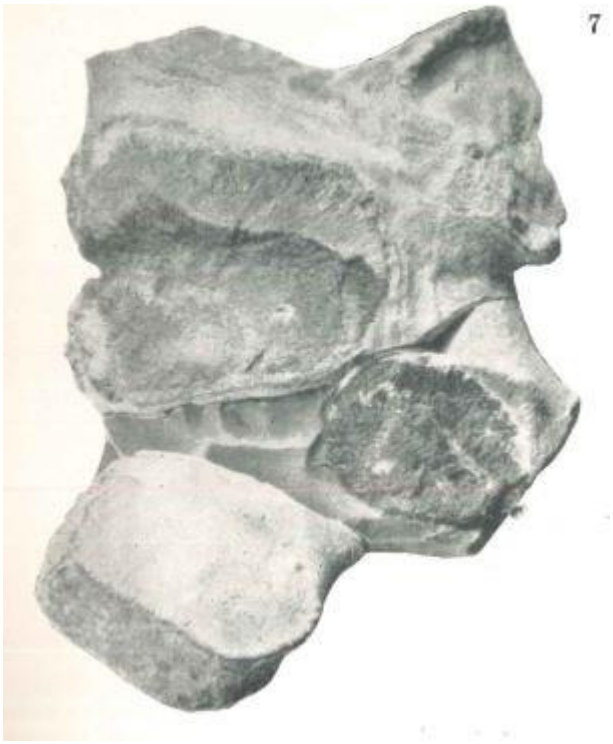

Figure 3.6.1: First documented historical picture of an element of MG 4747, identified as a radius and isolated ossicles of *S. uniter*, after Zbyszewski *et al.*, 1952.

New description

The specimen is composed of forelimb elements, which are flattened and plate-like. The radius, 54±5mm in length proximo-distally, 59±5mm in width antero-posteriorly, and 17±5mm thick dorso-ventrally, is wider than it is long and shows notching in the anterior face, while only a fragment of the ulna anterior face is observable. The intermedium, 30±5mm in length, 40±5mm in width and 11±5mm thick, is wider than it is long, with a straight proximal shape, and an apparently angular distal edge. The more isolated element is identified as the radial, 30±5mm in length, 48±5mm in width, and 22±5mm thick.

Phylogenetic analysis

Specimen MG 4747 yielded 50000 MPTs, each with a length of 1667 steps. The strict consensus is very poorly resolved, placing the specimen simultaneously in the species *Temnodontosaurus platyodon*, *Chacaiosaurus cayi*, *Leptonectes moorei*, and *Stenopterygius quadriscissus*, as well as in a basal position in the *Ichthyosaurus* clade and the clade of *L. solei* and *Excalibosaurus costini*, as well as the base of the Neoichthyosauria node (Figure 3.6.2).

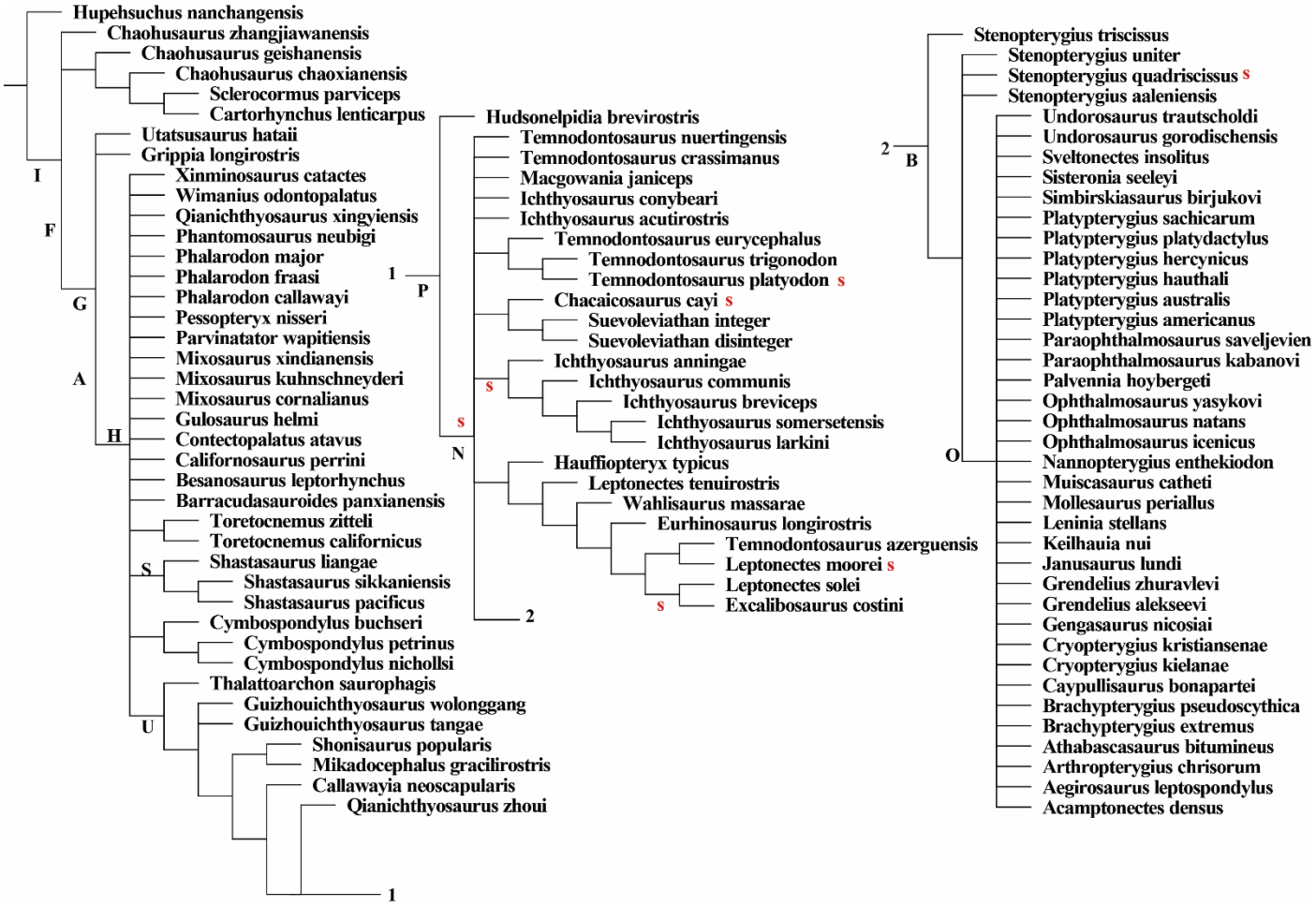

Figure 3.6.2: Strict consensus tree for specimen MG 4747, result of 50000 MPTs, 1667 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MG 37

Historical information

Referenced by: Zbyszewski *et al*, 1952.

Classified as: *Stenopterygius uniter*.

Locality: Pintanheira, S. Pedro de Moel.

Age: Pliensbachian (190.8-182.7 M.a).

Formation: Possibly Lemede formation.

Elements: Incomplete fin autopodium of nine ossicles organized in two rows, 140mm in length and 54mm in width.

Observations: Found associated with specimen MG 4747.

New description

The specimen, 50±5mm in width antero-posteriorly, 135±5mm in length, is composed of nine manual digits, 14±5mm in width, arranged in 2 rows, which become increasingly rounder distally.

Phylogenetic analysis

Specimen MG 37 yielded 50000 MPTs, each with a length of 1666 steps. The strict consensus is very poorly resolved, placing the specimen in 25 locations in the tree (Figure 3.7.1).

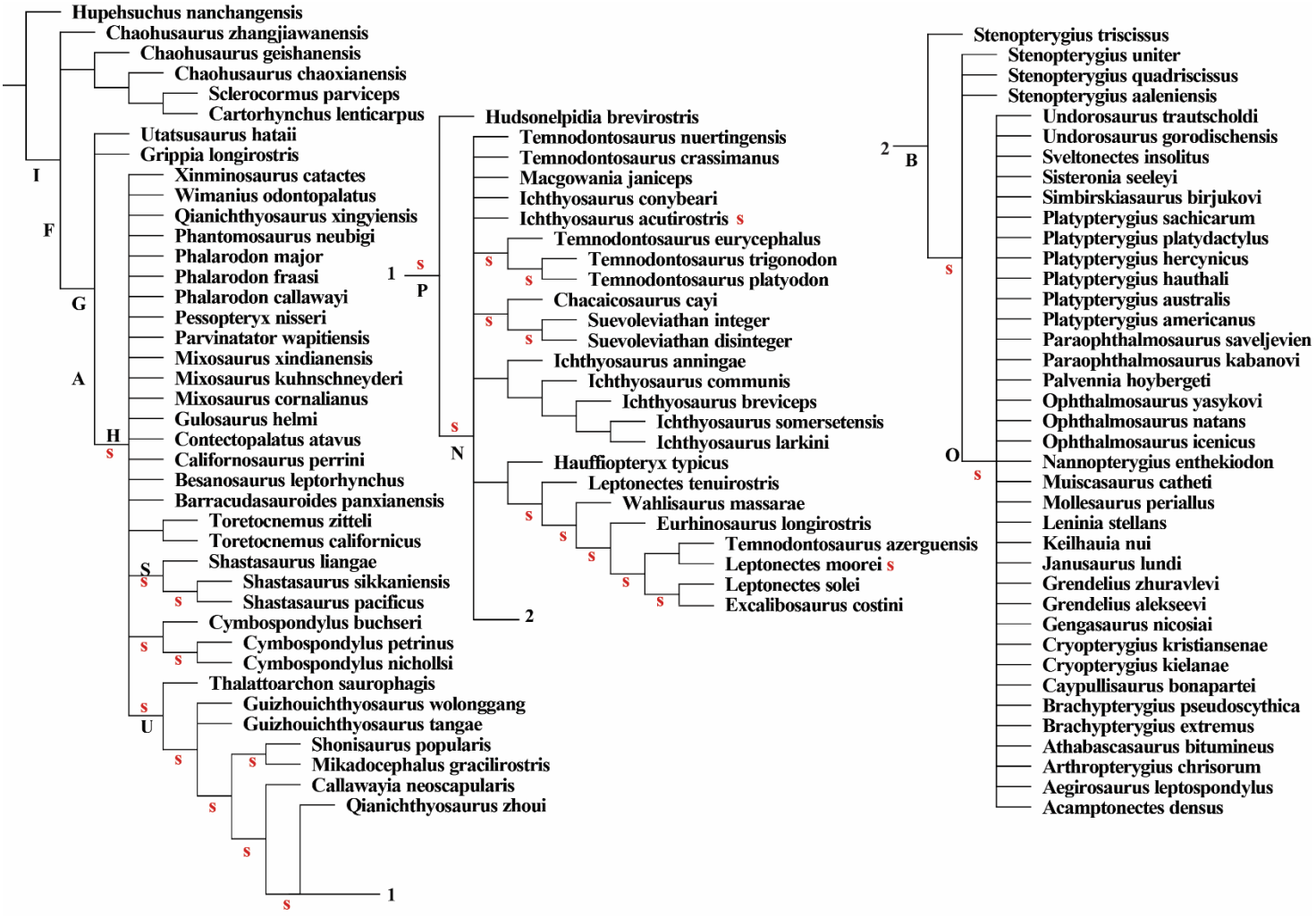

Figure 3.7.1: Strict consensus tree for specimen MG 37, result of 50000 MPTs, 1666 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MG 4750

Historical information

Referenced by: Zbyszewski *et al*, 1952.

Classified as: *Stenopterygius uniter*.

Locality: Pintanheira, S. Pedro de Moel.

Age: Pliensbachian (190.8-182.7 M.a).

Formation: Possibly Lemede formation.

Elements: Tip of a right femur, 68mm in length, 61mm in width.

New description

The specimen is composed of the tip of a block-shaped right femur, 35±5mm thick dorso-ventrally, 60±5mm in length proximo-distally, and 56±5mm in width antero-posteriorly, with the tibial and fibular facets being roughly subequal, while the shape of the fragment suggests the femur showed medial constriction.

Phylogenetic analysis

Specimen MG 4750 yielded 50000 MPTs, each with a length of 1666 steps. The strict consensus is very poorly resolved, placing the specimen in 20 locations in the tree (Figure 3.8.1).

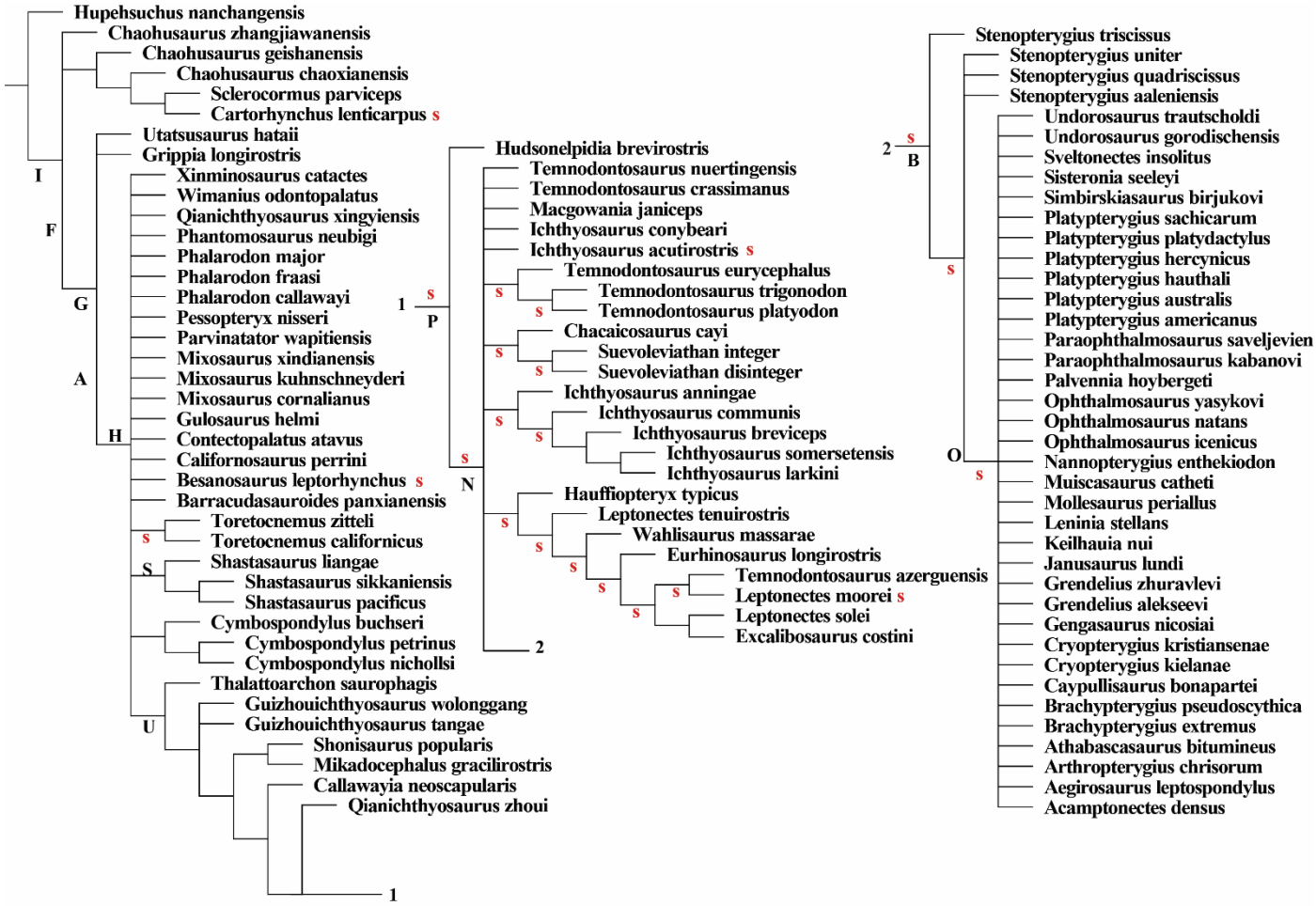

Figure 3.8.1: Strict consensus tree for specimen MG 4750, result of 50000 MPTs, 1666 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MG 4755

Historical information

Referenced by: Zbyszewski *et al*, 1952.

Classified as: *Stenopterygius uniter*.

Locality: Pintanheira, S. Pedro de Moel.

Age: Pliensbachian (190.8-182.7 M.a).

Formation: Possibly Lemede Formation.

Elements: A set of 38 flattened precaudal vertebrae, with a length ranging from 28 to 33mm, a height ranging from 60 to 72mm, and a width of 70mm (Zbyszewski *et al*, 1952).

New description

The specimen is composed of 38 vertebrae, likely dorsal, some of which articulated, but the specimen is covered in sediment that makes character identification difficult.

Phylogenetic analysis

An analysis was not performed for this specimen on account of not enough characters being determined.

MG 4751

Historical information

Referenced by: Zbyszewski *et al*, 1952.

Classified as: *Stenopterygius uniter*.

Locality: Pintanheira, S. Pedro de Moel.

Age: Pliensbachian (190.8-182.7 M.a).

Formation: Lias, possibly Lemede Formation.

Elements: Various jaw fragments, one with an imprint of a big, striated conic tooth, and several broken fragments of teeth; The teeth have a conic tip, extending downwardly to a subcylindrical body with streaks and grooves (Figure 3.10.1) (Zbyszewski *et al*, 1952).

Figure 3.10.1: First documented historical picture of one of the jaw fragments of MG 4751, identified as *S. uniter* after Zbyszewski *et al.*,

New description

The specimen is composed of two jaw fragments, one with a large tooth impression, that implies a well-developed dentition, and several broken teeth fragments. The teeth are conical, ornamented with prominent ridges and grooves, and subtle striations are visible at the roots.

Phylogenetic analysis

Specimen MG 4751 yielded 24640 MPTs, each with a length of 1667 steps. The strict consensus is poorly resolved, placing the specimen in the species *T. crassimanus*, in a basal position in the clade of *I. larkini* and *I. somersetensis*, and at the base of the Ophthalmosauridae node (Figure 3.10.2).

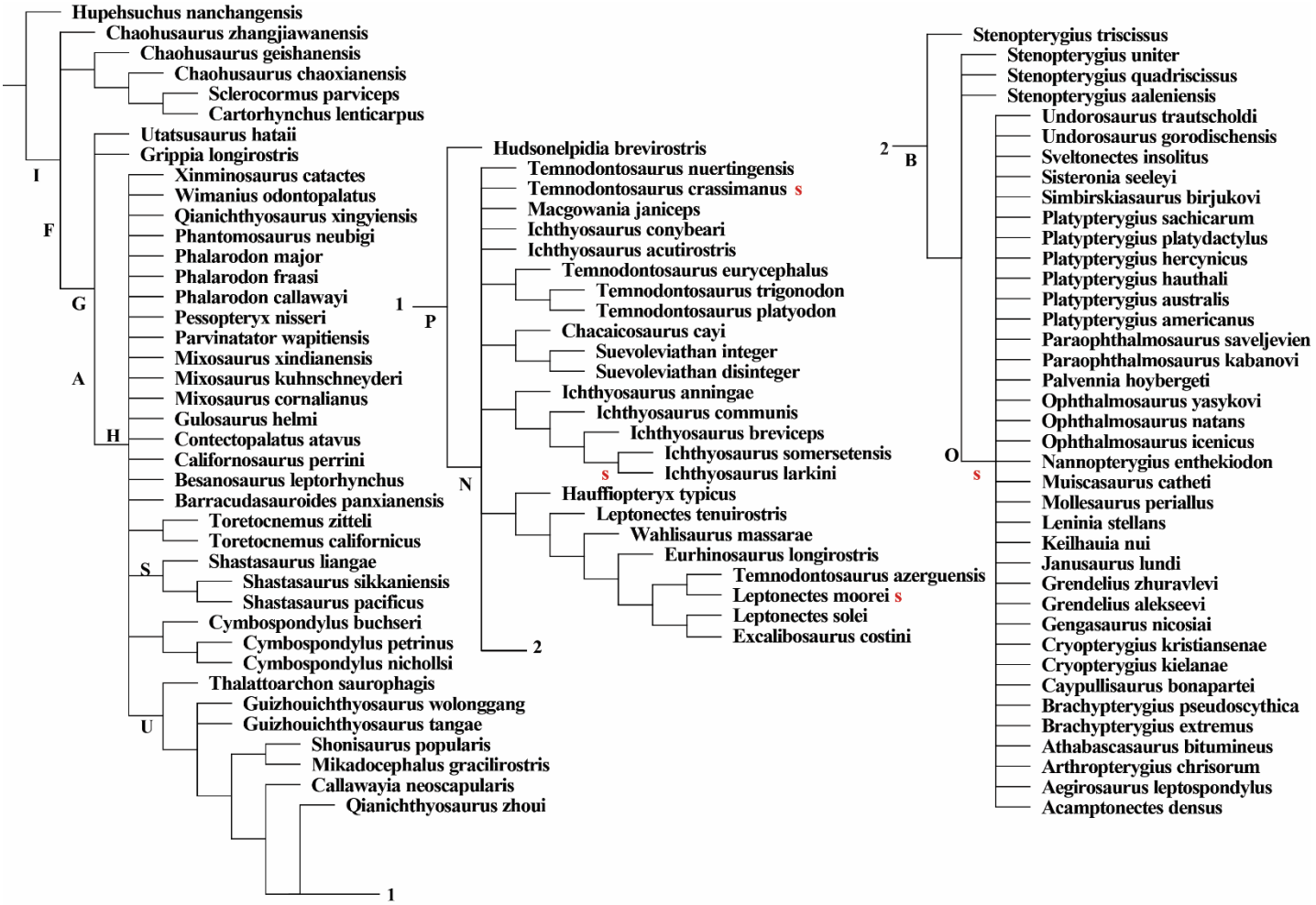

Figure 3.10.2: Strict consensus tree for specimen MG 4751, result of 24640 MPTs, 1667 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MG 25184

Historical information

Referenced by: Veiga Ferreira, 1958.

Classified as: *Ichthyosaurus intermedius.*

Locality: Alvaiázere.

Age: Pliensbachian (190.8-182.7 M.a).

Formation: Undetermined.

Elements: A single vertebra, with a diameter of 50x55mm, and a width of 25mm (Veiga Ferreira, 1958).

New description

The specimen is composed of a single, poorly preserved vertebra. The centrum is short and equally as long as it is wide (Figure 3.11.1).

Figure 3.11.1: MG 25184 (Pictures by Octávio Mateus), composed of a single vertebra. 1-Dorsal view; 2-Anterior view; 3-Posterior view; 4-Ventral view. Bar marks 2 cm.

Phylogenetic analysis

Specimen MG 25184 yielded 50000 MPTs, each with a length of 1666 steps. The strict consensus is poorly resolved, placing the specimen simultaneously in the species *E. longirostris*, in a basal position between the *Stenopterygius* clade and the Ophthalmosauridae node, as well as at the base of this last one (Figure 3.11.2).

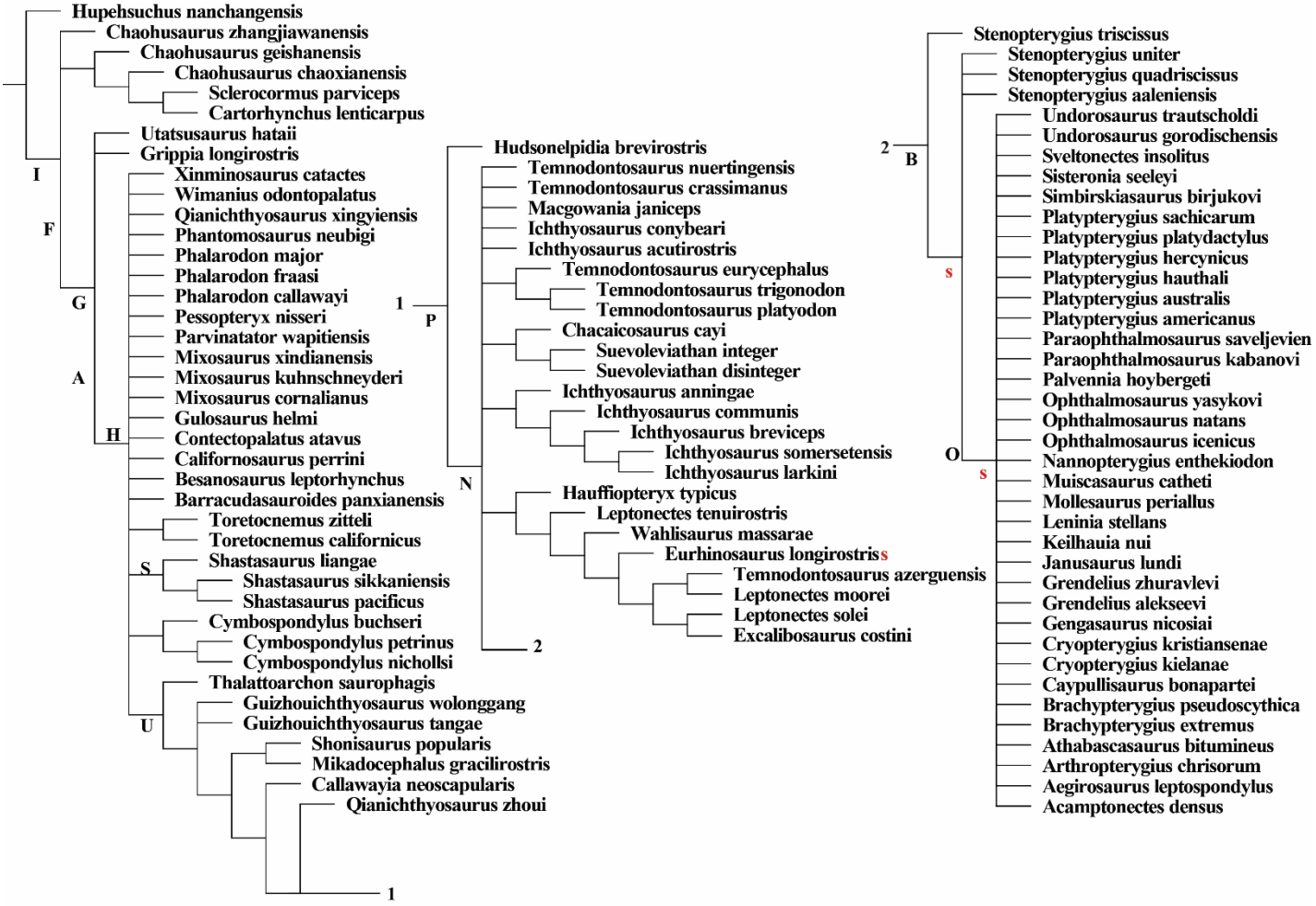

Figure 3.11.2: Strict consensus tree for specimen MG 25184, result of 50000 MPTs, 1666 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

TOARCIAN

MG 25182 and MG 25183

Historical information

Referenced by: Veiga Ferreira, 1958.

Classified as: *Stenopterygius sp.*

Locality: Condeixa.

Age: Toarcian (182.7-174.1 M.a).

Formation: Possibly S. Gião Formation.

Elements: Two sets of dorsal vertebrae from Liassic limestones, 15 (MG 25182) and 13 vertebrae (Mg 25183) each, with diameters ranging from 95x82mm to 75x70mm and a width of 35mm (Veiga Ferreira, 1958).

Observations: Ammonites identified as *Polyplectus discoides* and *Harpoceras serpentinum* were found affixed to vertebrae from these two sets. The specimens are noted to be poorly preserved, due to which a species could not be determined (Figure 3.12.1).

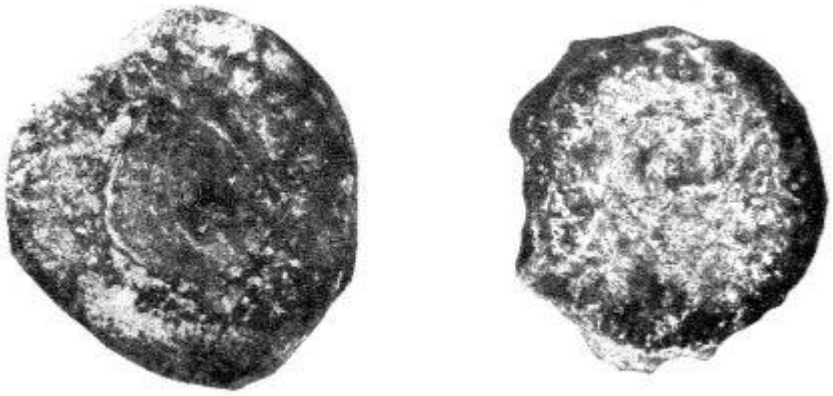

Figure 3.12.1: First documented historical pictures of a dorsal vertebra from the MG 25182 and MG 25183 sets, identified as sets of dorsal vertebrae of *Stenopterygius sp.*, after Veiga Ferreira, 1958.

New description

These two specimens are composed of two sets of dorsal vertebrae, 15 and 13 respectively, notably poorly preserved, and in both of them one vertebra shows imprints of ammonites affixed to it, identified as *Polyplectus discoides* and *Harpoceras serpentinum.* The vertebrae all seem to be less than 3.5 times as high as they are long, and they all have roughly equal height (Figure 3.12.2 and .3).

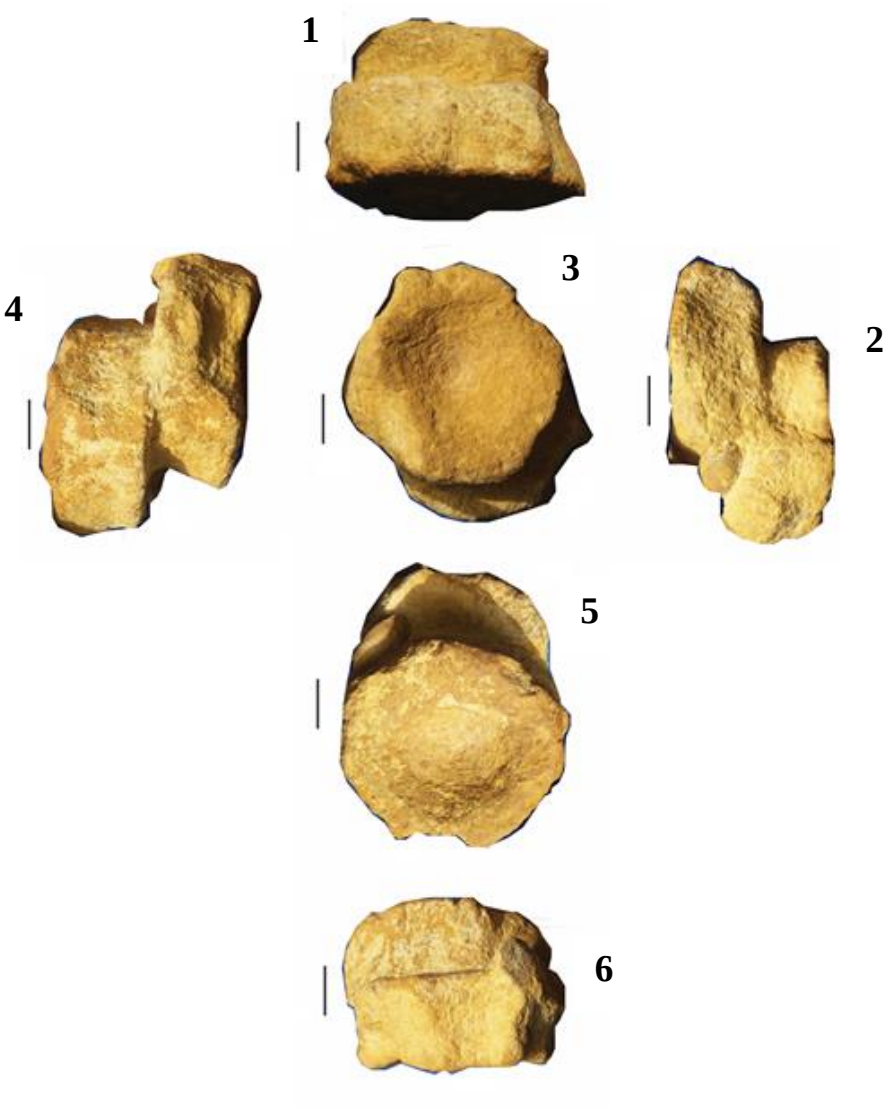

Figure 3.12.2: Two of the 15 dorsal vertebra set of MG 25182 (Pictures by Octávio Mateus). 1-Dorsal view; 2-Left view; 3-Anterior view; 4-Right view; 5-Posterior view; 6-Ventral view. Bar marks 2cm.

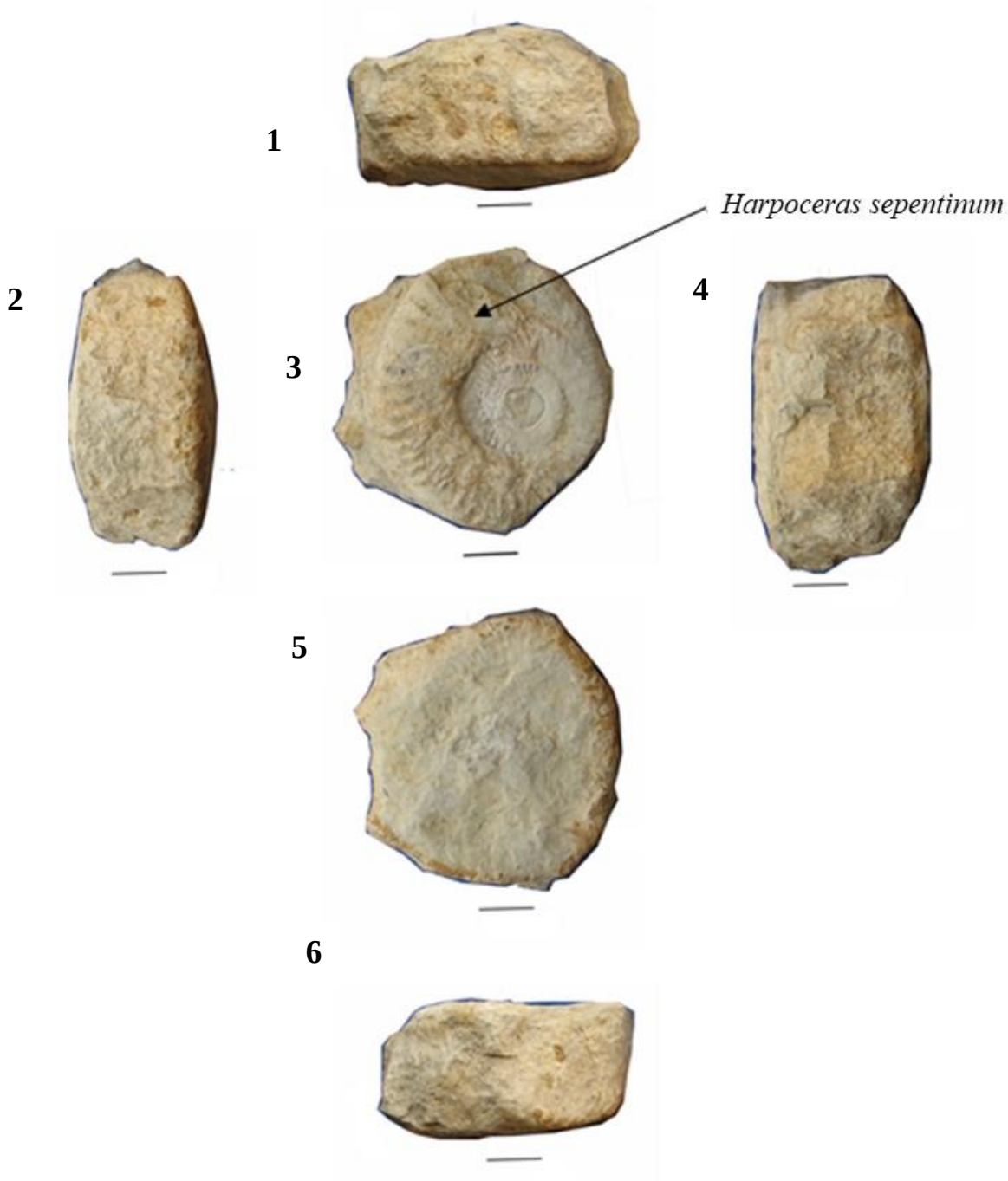

Figure 3.12.3: One of the 13 dorsal vertebra of MG 25183 (Pictures by Octávio Mateus), showing an imprint of *Harpoceras serpentinum*. 1-Dorsal view; 2-Left view; 3-Anterior view; 4-Right view; 5-Posterior view; 6-Ventral view. Bar marks 2 cm.

Phylogenetic analysis

The analyses for these 2 specimens yielded 50000 MPTs, each with a length of 1666 steps, for both. The strict consensus is very poorly resolved, with MG 25182 being placed in 14 locations in the tree, while MG 25183 was placed in 16 (Figure 3.12.4).

Figure 3.12.4: Strict consensus trees for specimen MG 25182 (top) and MG 25183 (bottom), result of 50000 MPTs, 1666 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

AALENIAN

MG 4743

Historical information

Referenced by: Veiga Ferreira, 1958.

Classified as: *Stenopterygius uniter*.

Locality: Tomar.

Age: Aalenian (174.1-170.3 M.a).

Formation: Possibly Formação de Coimbra.

Elements: A dorsal vertebra, with a height of 75mm, a length of 65mm and a width of 17mm (Figure 3.13.1). (Veiga Ferreira, 1958).

Observation: Noted to be similar to the vertebrae found in Pintanheira.

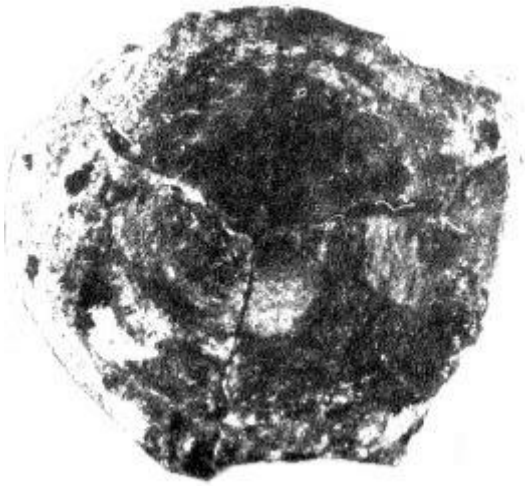

Figure 3.13.1: First documented historical picture of specimen MG 4743, identified as a dorsal vertebra of *S. uniter* after Veiga Ferreira, 1958.

New description

This specimen is composed of a single dorsal vertebra. It is missing from the collection of the Museu Geológico de Lisboa, and the only picture of it on record is of very poor quality.

Phylogenetic analysis

Specimen MG 4743 could not be found, and so an analysis was not performed.

MG 36

Historical information

Referenced by: Sauvage, 1898.

Classified as: *Stenopterygius uniter*.

Locality: Alhadas.

Age: Aalenian (174.1-170.3 M.a).

Formation: Possibly Formação de Coimbra, Camadas de São Miguel.

Elements: Jaw fragments with long cylindrical teeth, 15mm, with striations that are more evident at the roots (Figure 3.14.1) (Sauvage, 1898).

Observation: This specimen has been first referenced by Sauvage, and later mentioned by Zbyszewski, but it was considered incerta sedis and only classified as *S. uniter* by Castanhinha and Mateus in 2007.

Figure 3.14.1: Historical Picture of specimen MG 36, identified as maxillary fragments of *S. uniter* after Zbyszewski *et al.*, 1952.

New description

The specimen is composed of a snout fragment, 55±5mm in height, with an upper jaw 86±5mm in length and 35±5mm in width, and a lower jaw 80±5mm in length and 30±5mm in width, and teeth with 20±5mm in length. The lower jaw is well-developed but not slenderer than the upper jaw, and its ventral margin is seemingly concave, and a labial shelf in the dental is not observable. Around ten teeth are observable, well-developed, with aulacodont implantation in a single row, with an upper and lower dental groove throughout the visible jaw. No palatine or pterygoidal teeth are observable, and tooth replacement seems to be regular. The enamel is decorated with prominent ridges

and grooves, while the roots are round and decorated with subtle striations, and the tooth crowns are circular (Figure 3.14.2).

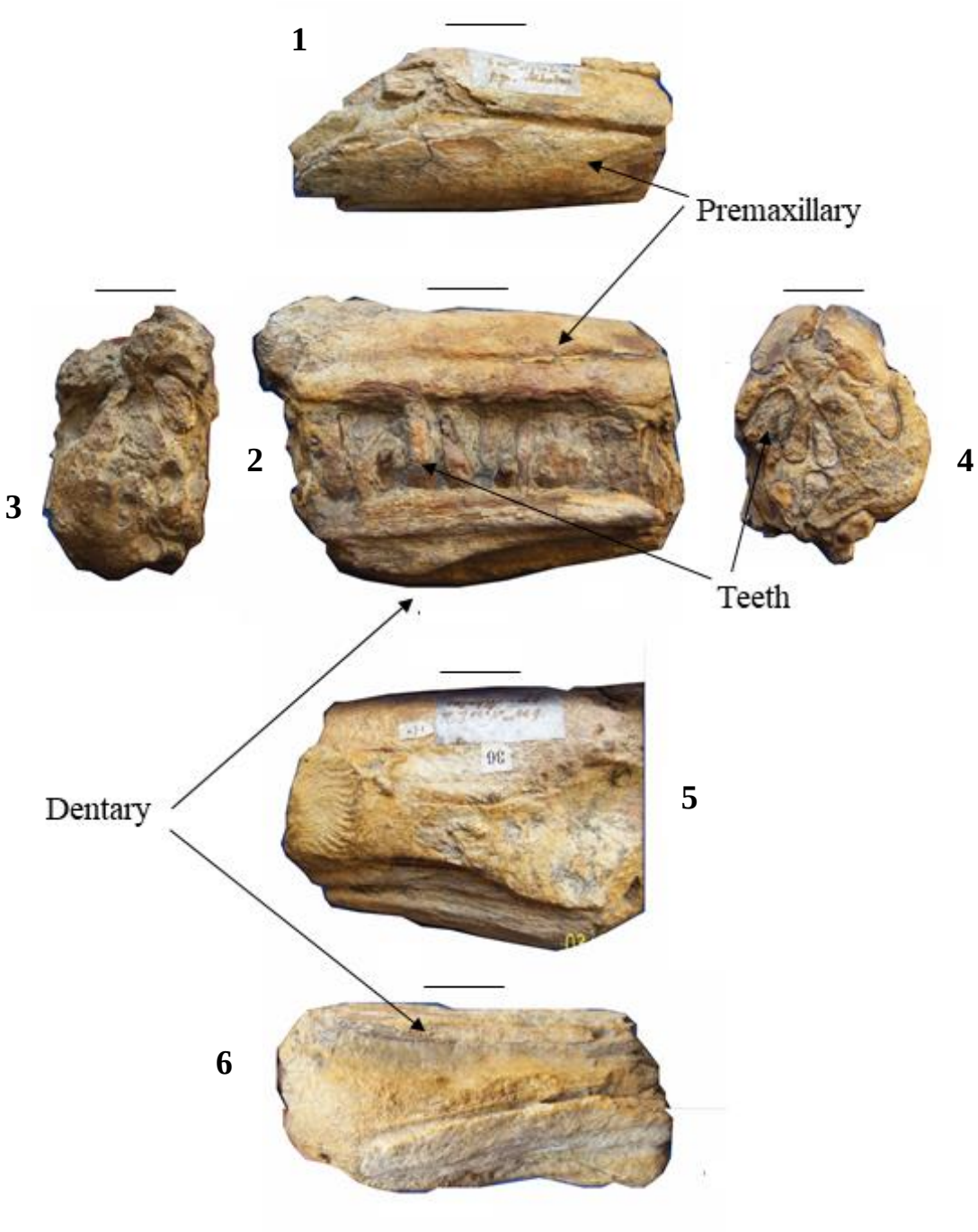

Figure 3.14.2: MG 36 (Pictures by Octávio Mateus), composed of tooth-bearing maxillary fragments. 1-Dorsal view; 2-Right view; 3-Posterior view; 4 -Anterior view ; 5-Left view; 6-Ventral view. Bar marks 2 cm.

Specimen MG 36 yielded 17548 MPTs, each with a length of 1668 steps. The strict consensus is poorly resolved, placing the specimen in the species *Phalarodon fraasi*, and at the base of the Hueneosauria and Shastasauria nodes (Figure 3.14.3)

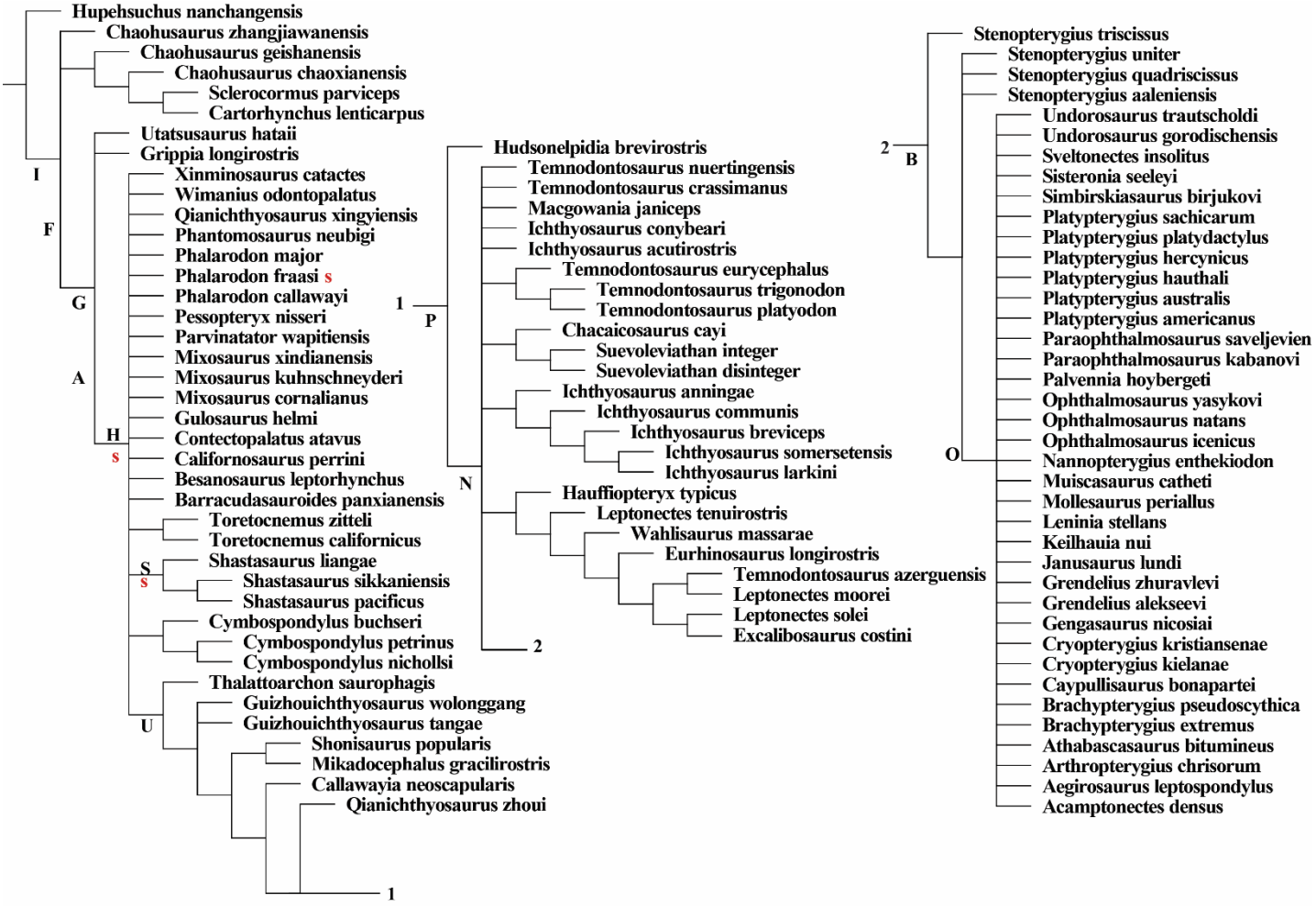

Figure 3.14.3: Strict consensus tree for specimen MG 36, result of 17548 MPTs, 1668 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MG 4753

Historical information

Referenced by: Veiga Ferreira, 1958.

Classified as: *Stenopterygius.*

Locality: Tomar.

Age: Aalenian (174.1-170.3 M.a).

Formation: Possibly Formação de Coimbra.

Elements: A caudal vertebra, with a diameter of 40x35mm and a width of 17mm (Figure 36) (Veiga Ferreira, 1958).

New description

The specimen is composed of a single, deformed caudal vertebra. Not much else is observable (Figure 3.15.1).

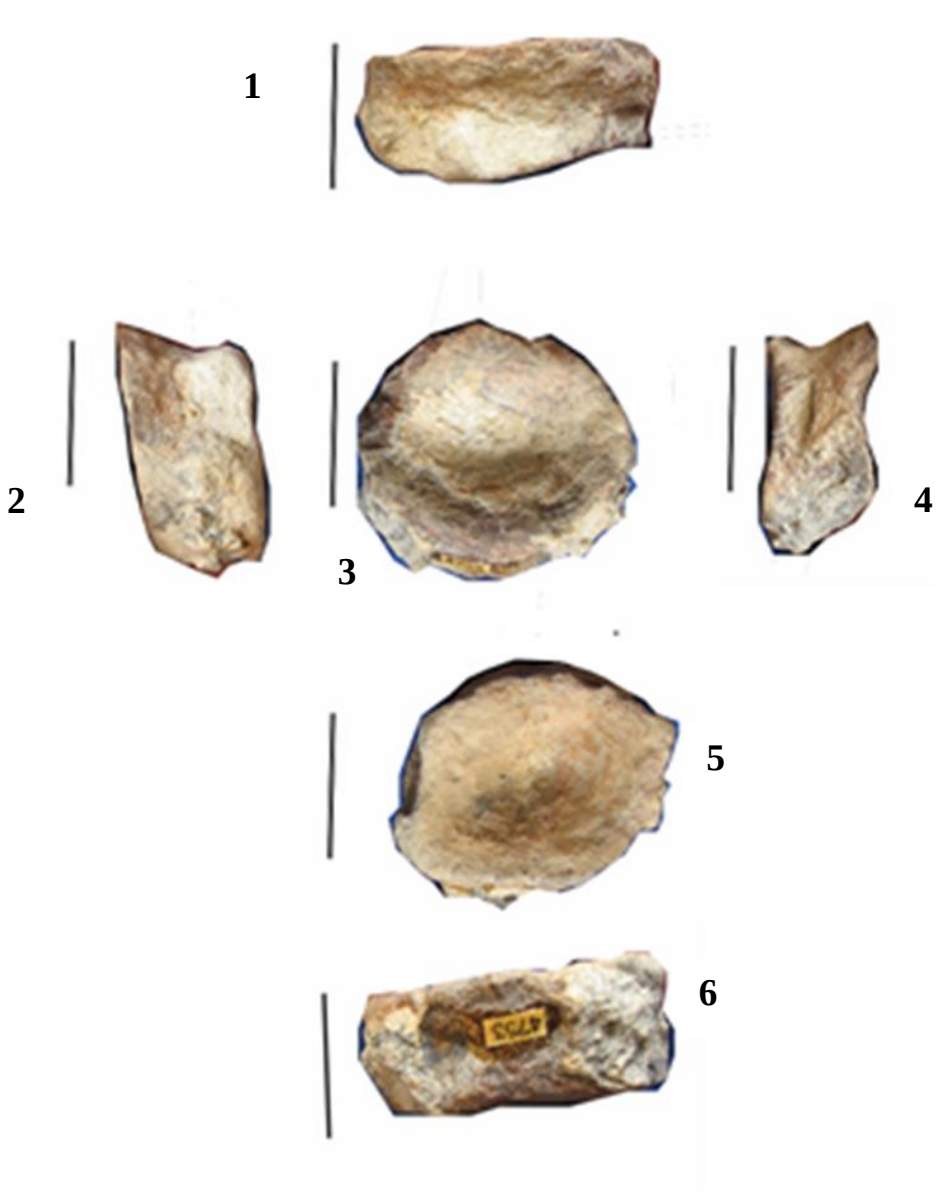

Figure 3.15.1: MG 4753 (Pictures by Octávio Mateus), comprised of a single caudal vertebra. 1-Dorsal view; 2-Left view; 3-Anterior view; 4-Right view; 5-Posterior view; 6-Ventral view. Bar marks 2cm.

Phylogenetic analysis

Specimen MG 4753 yielded 50000 MPTs, each with a length of 1666 steps. The strict consensus is very poorly resolved, placing the specimen in 30 locations in the tree (Figure 3.15.2).

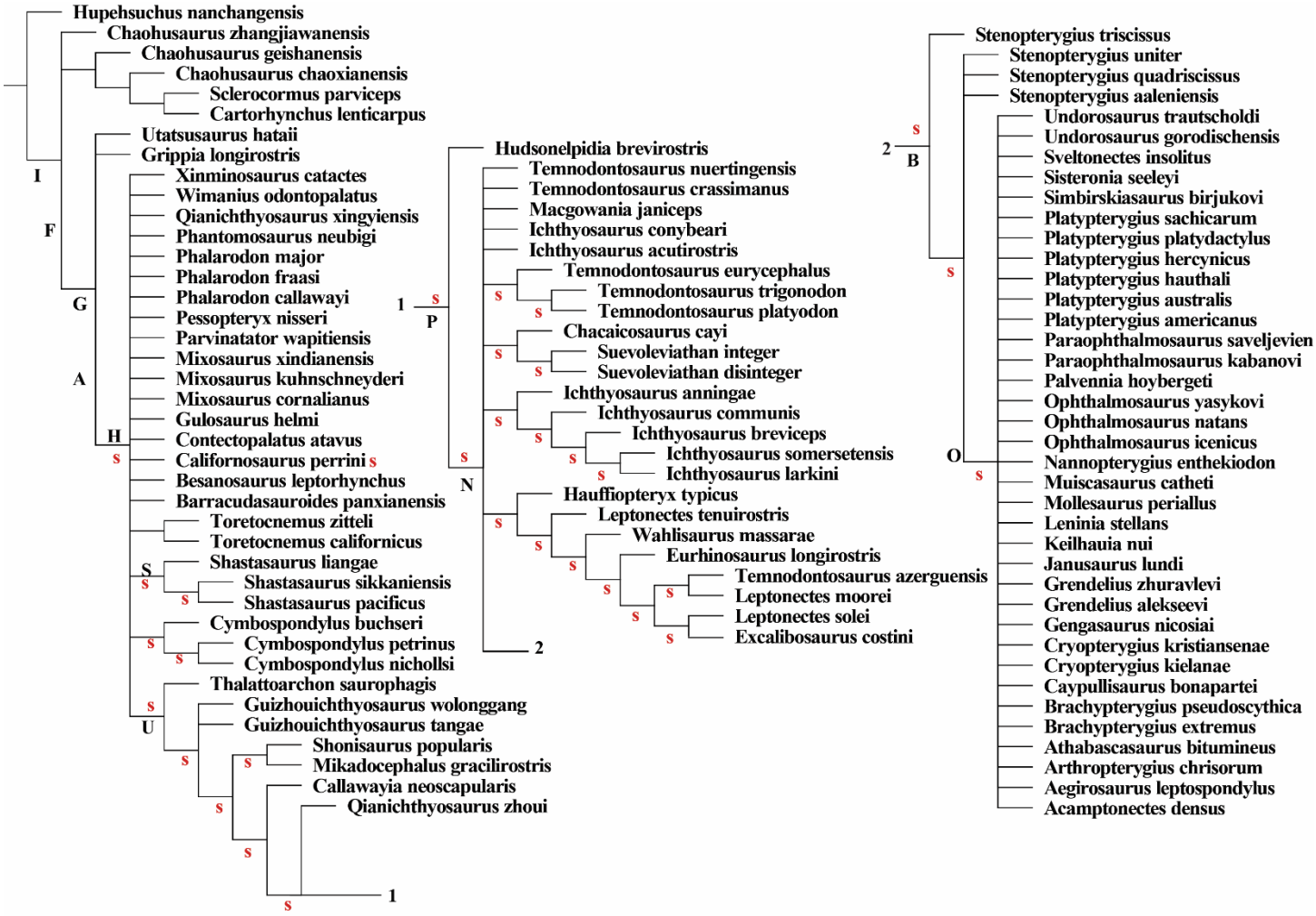

Figure 3.15.2: Strict consensus tree for specimen MG 4753, result of 50000 MPTs, 1666 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

UNCERTAIN AGE

MG 4746

Historical information

Referenced by: Veiga Ferreira, 1958.

Classified as: *Ichthyosaurus intermedius.*

Locality: Casal Comba.

Age: Possibly Pliensbachian (190.8-182.7 M.a).

Formation: Possibly Formação de S. Gião.

Elements: A set of two small caudal vertebrae, with a diameter of 12x11mm (Figure 3.16.1). (Veiga Ferreira, 1958).

Figure 3.16.1: First documented historical picture of MG 4746, identified as two caudal vertebras of *I. intermedius* after Veiga Ferreira, 1958.

New description

The specimen is composed of two small caudal vertebrae, with short centra, roughly 13 mm antero-posteriorly, as wide as they are high (Figure 3.16.2).

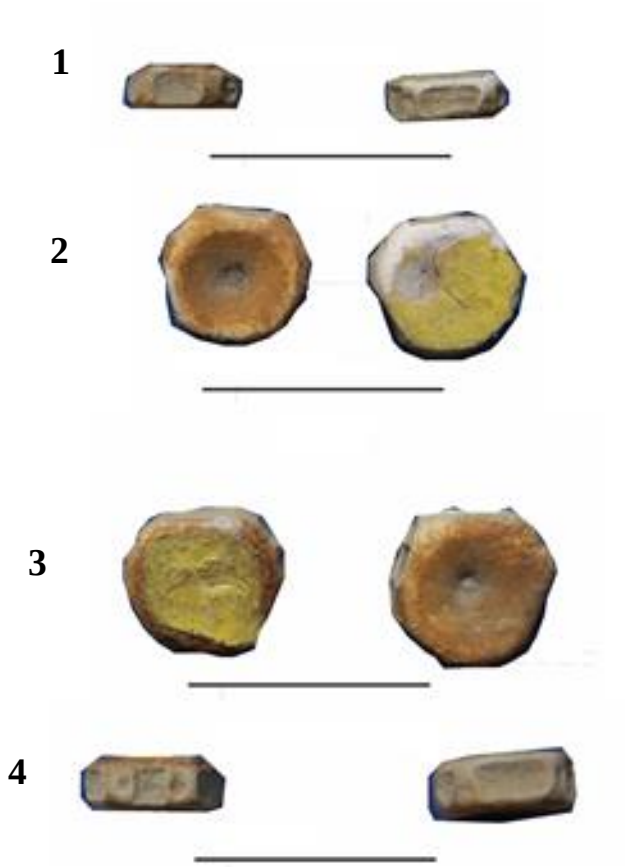

Figure 3.16.2: MG 4746 (Pictures by Octávio Mateus), comprised of two caudal vertebrae. 1-Dorsal view; 2-Anterior view; 3-Posterior view; 4-Ventral view. Bar marks 2 cm.

Phylogenetic analysis

Specimen MG 4746 yielded 50000 MPTs, each with a length of 1666 steps. The strict consensus, like MG 25184, is poorly resolved, placing the specimen in the species *E. longirostris*, in a basal position between the *Stenopterygius* clade and the Ophthalmosauridae node, as well as at the base of this last one (Figure 3.16.3).

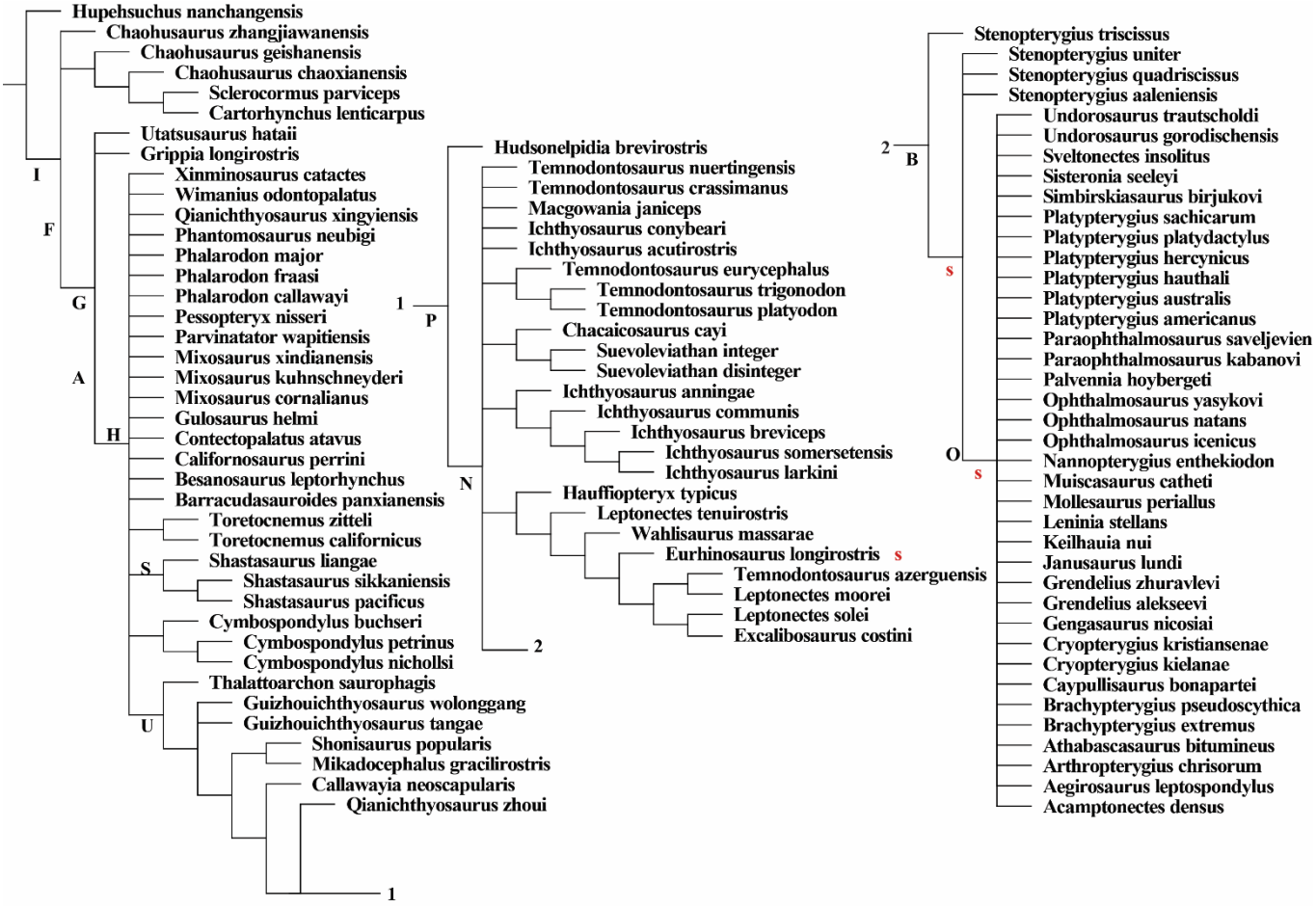

Figure 3.16.3: Strict consensus tree for specimen MG 4746, result of 50000 MPTs, 1666 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MG 4748

Historical information

Referenced by: Veiga Ferreira, 1958.

Classified as: *Ichthyosaurus intermedius.*

Locality: Águas de Madeiros, S. Pedro de Moel.

Age: Possibly Sinemurian (199.3-190.3 M.a).

Formation: Possibly Formação de Coimbra.

Elements: A set of two vertebrae, with diameters of 18x19 and 13x13mm (Figure 3.17.1).

(Veiga Ferreira, 1958).

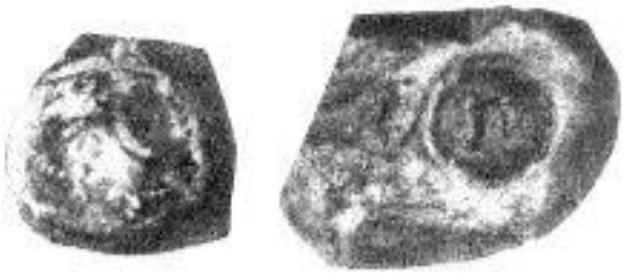

Figure 3.17.1: First documented historical picture of MG 4748, identified as two vertebra of *I. intermedius*, after Veiga Ferreira, 1958.

New description

The specimen is composed by two small vertebrae, which through comparison with other specimens are identified as caudal, and with short centra, roughly 18 and 13mm antero-posteriorly, as wide as they are high.

Phylogenetic analysis

Specimen MG 4748 yielded 50000 MPTs, each with a length of 1666 steps. The strict consensus is poorly resolved, like previous specimens placing the MG 4748 in the species *E. longirostris*, in a basal position between the *Stenopterygius* clade and the Ophthalmosauridae node, as well as at the base of this last one (Figure 3.17.2).

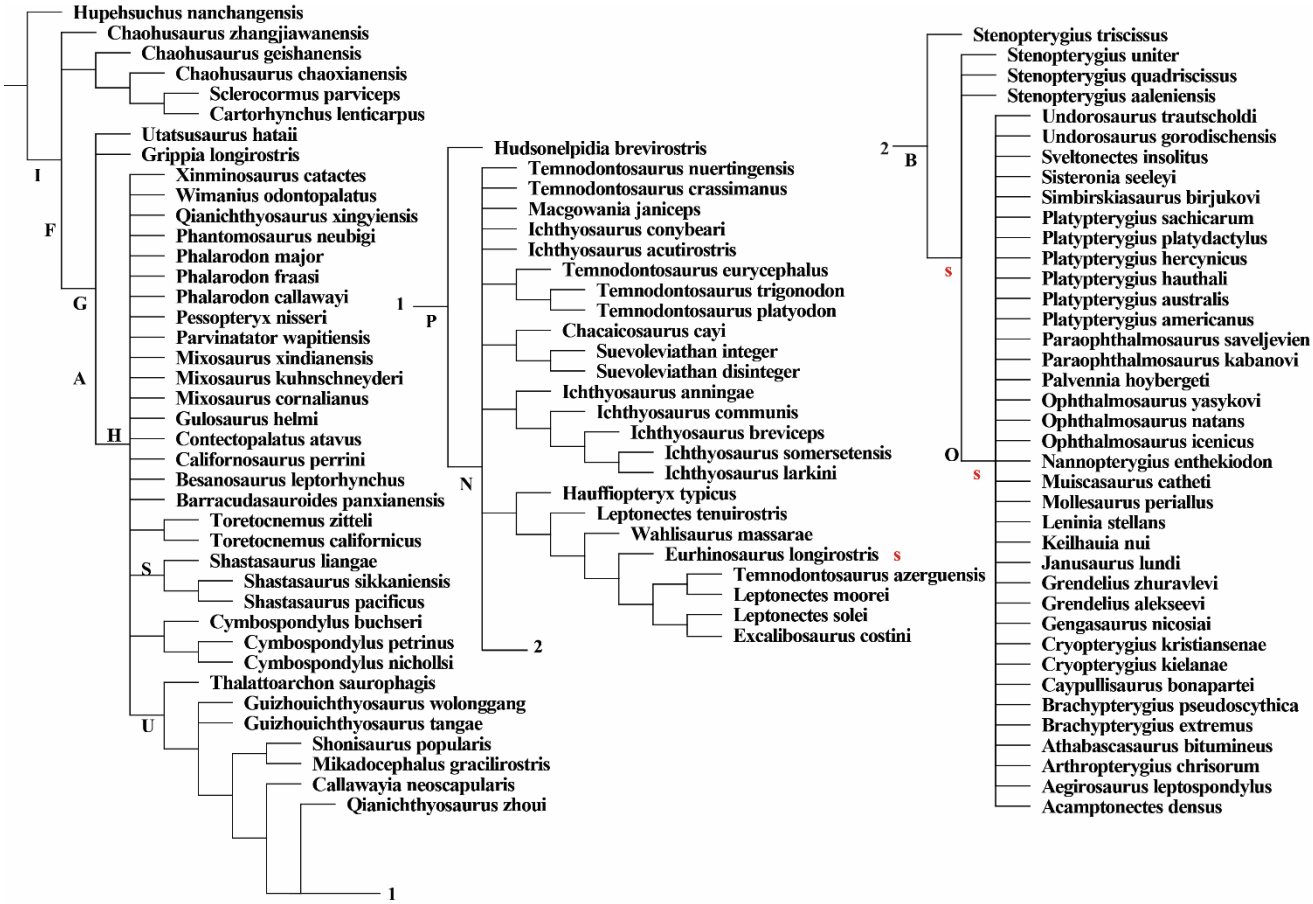

Figure 3.17.2: Strict consensus tree for specimen MG 4748, result of 50000 MPTs, 1666 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MG 4752

Historical information

Referenced by: Castanhinha and Mateus., 2007.

Classified as: *Ichthyosaurus sp.*

Locality: Cadima.

Age: Lower Jurassic.

Formation: Formação do Lemede.

Elements: A set of three articulated caudal vertebrae, with a width of 38mm, a height of 35.5mm (Figure 3.18.1) (Zbyszewski *et al*, 1952).

Observations: The specimen was considered Incerta sedis by Zbyszewski, in 1952 and was only classified by Castanhinha and Mateus in 2007.

Figure 3.18.1: First documented historical picture of MG 4752, identified as three articulated caudal vertebrae of *Ichthyosaurus sp.*, after Zbyszewski *et al*, 1958

New description

The specimen is composed a set of three articulated vertebrae. The centra are as wide as they are high, with short, roughly 12mm, and wide spinous processes (Figure 3.18.2).

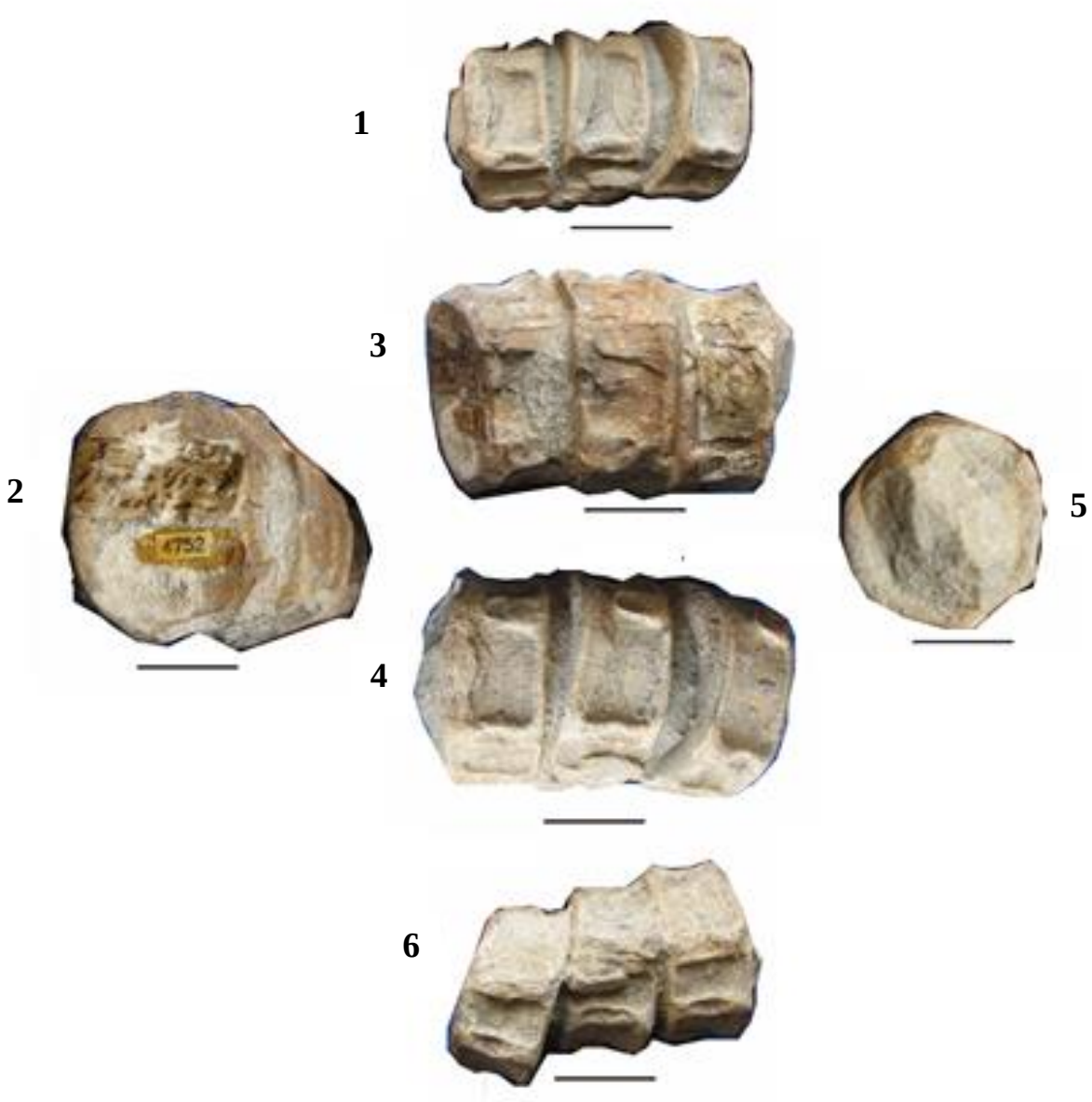

Figure 3.18.2: MG 4752 (Pictures by Octávio Mateus), comprised of a set of three articulated caudal vertebra. 1-Dorsal view; 2-Anterior view; 3-Left view; 4-Right view; 5-Posterior view; 6-Ventral view. Bar marks 2 cm.

Phylogenetic analysis

Specimen MG 4752 yielded 50000 MPTs, each with a length of 1667 steps. The strict consensus, like previous specimens, is poorly resolved, placing the specimen in the species *E. longirostris*, in a basal position between the *Stenopterygius* clade and the Ophthalmosauridae node, as well as at the base of this last one (Figure 3.18.3).

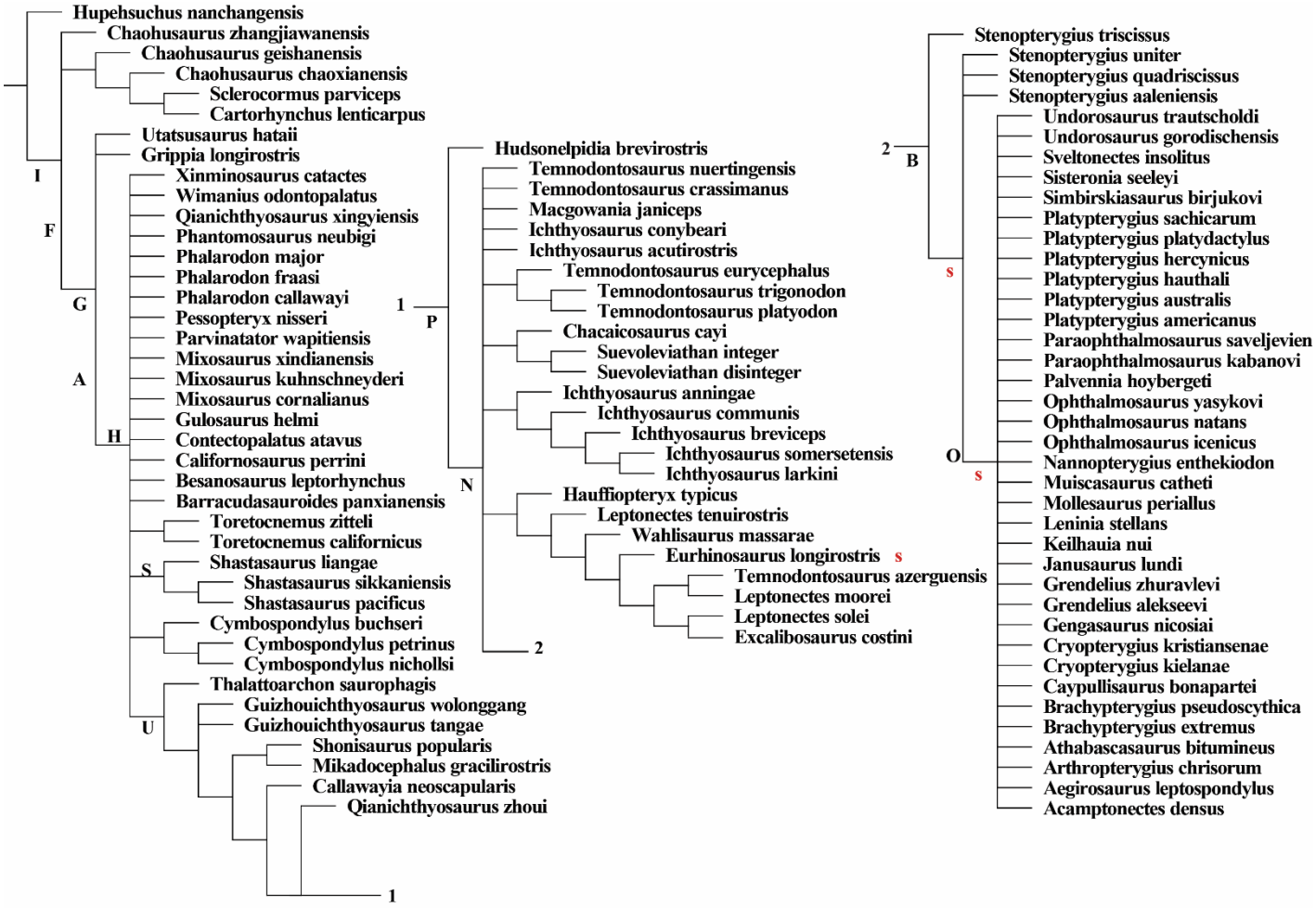

Figure 3.18.3: Strict consensus tree for specimen MG 4752, result of 50000 MPTs, 1667 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MG 35

Historical information

Referenced by: Castanhinha and Mateus., 2007.

Classified as: *Ichthyosaurus*

Locality: Murtede

Age: Possibly Aalenian (174.1-170.3 M.a).

Formation: Formação de S. Gião.

Elements: Several maxillary fragments with sub-cylindrical teeth sporting thin striations, with a length of around 30mm (Figure 3.19.1). (Zbyszewski *et al*, 1952).

Observations: This specimen has been mentioned as incerta sedis by Zbyszewski before being classified by Castanhinha and Mateus (2007).

Figure 3.19.1: First documented historical picture of MG 35, identified as one of the maxillary fragments of *Ichthyosaurus*¸ after Zbyszewski *et al*, 1958.

New description

The specimen is composed of two maxillary fragments, sporting around 4 well-developed teeth displayed in a single row, with conical crowns. The enamel is decorated with prominent ridges and grooves, and the base is not discernible, while the roots show subtle striation marks (Figure 3.19.2).

Figure 3.19.2: MG 35(Pictures by Octávio Mateus), composed of two tooth-bearing maxillary fragments. Bar marks 2 cm.

Phylogenetic analysis

Specimen MG 35 yielded 50000 MPTs, each with a length of 1666 steps. The strict consensus is very poorly resolved, placing the specimen in 14 locations in the tree (Figure 3.19.3).

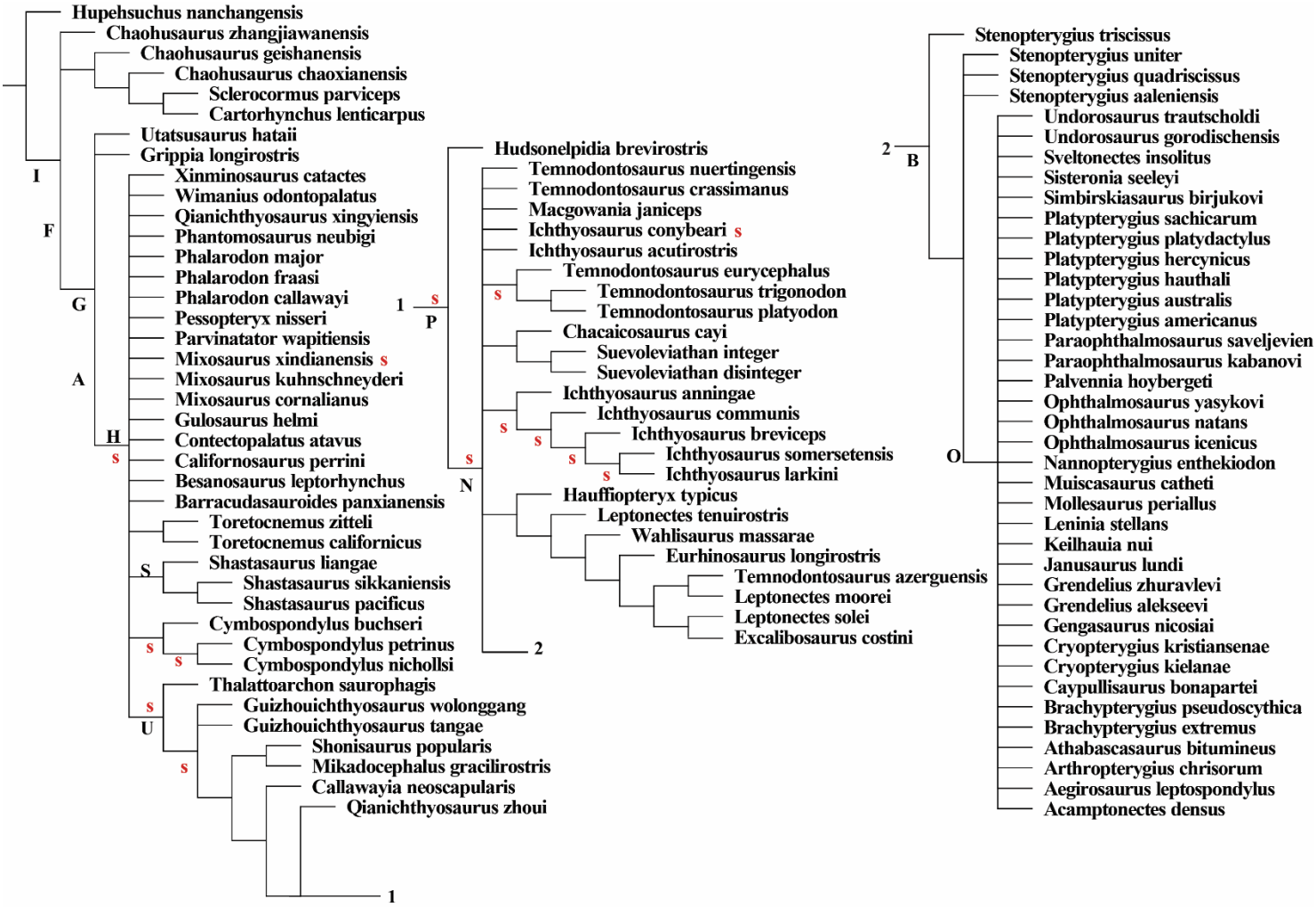

Figure 3.19.3: Strict consensus tree for specimen MG 35, result of 50000 MPTs, 1666 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

MG 25186

Historical information

Referenced by: Castanhinha and Mateus., 2007.

Classified as: *Stenopterygius uniter*

Locality: Undetermined

Age: Undetermined

Formation: Undetermined

Elements: 2 blocks with rib and vertebrae fragments.

New description

The specimen is composed of two blocks, containing several fragments of vertebrae and ribs.

Phylogenetic analysis

Specimen MG 26186 yielded 50000 MPTs, each with a length of 1666 steps. The strict consensus is very poorly resolved, placing the specimen in 19 locations in the tree (Figure 3.20.1).

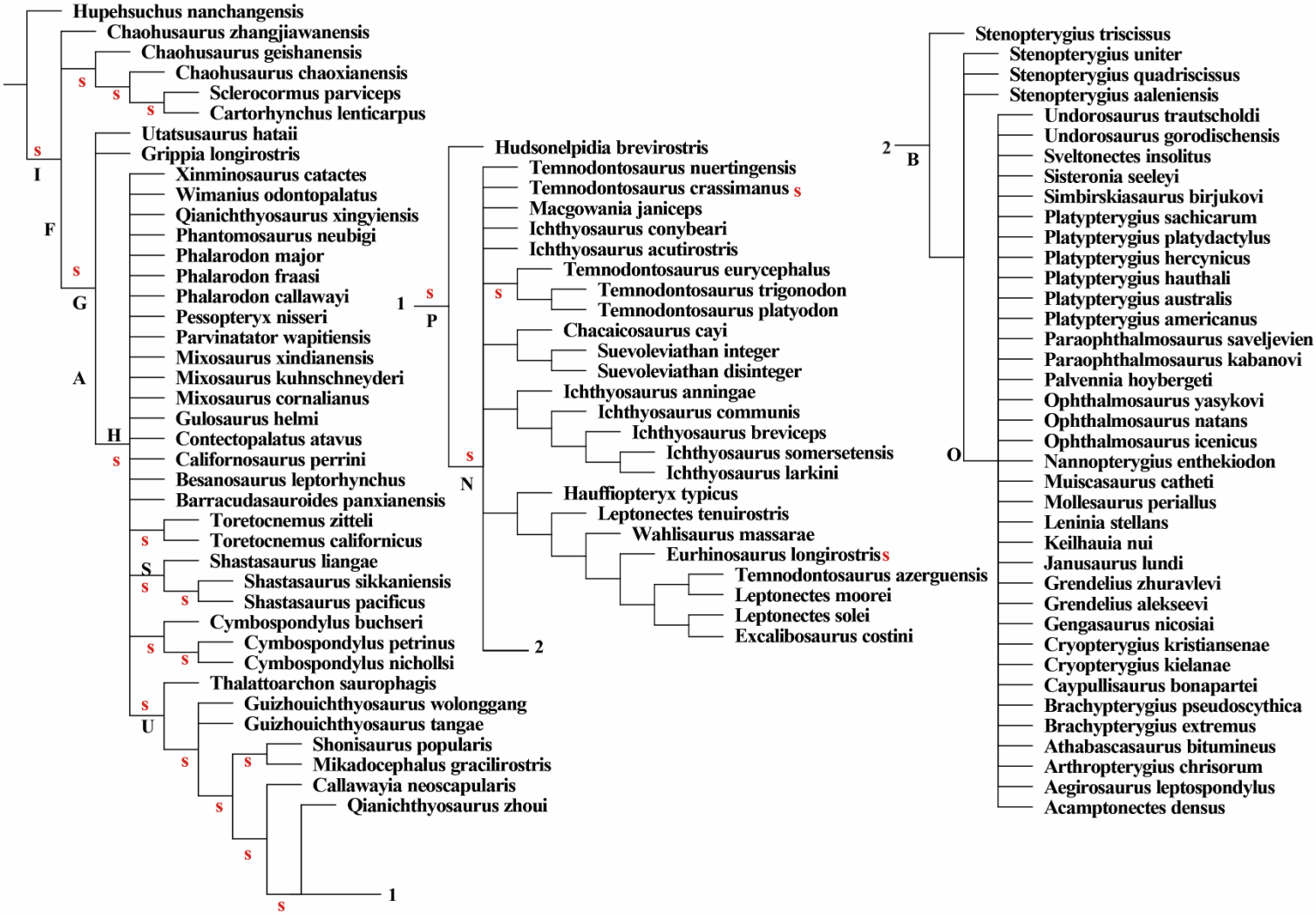

Figure 3.20.1: Strict consensus tree for specimen MG 25186, result of 50000 MPTs, 1667 steps. A-Ichthyosauria, B-Baracromia, F-Ichthyosauriformes, G-Ichthyopterygia, H-Hueneosauria, I-Ichthyosauromorpha, N-Neoichthyosauria, O-Ophthalmosauridae, P-Parvipelvia, S-Shastasauria, U-Euichthyosauria, s-specimen.

DISCUSSION

Descriptions

The historical descriptions from when the ichthyosaur specimens of the Portuguese fossil record were first documented are lacking in detail. As a part of this study, the specimens were observed, and new descriptions were made, based on the list of characters compiled by Moon, (2017). Despite a difficulty in observing and sometimes interpreting different characters, a more complete description of the specimens was made, and in the case of most specimens, the new description is in line with what was historically observed, but there is one case that stands out.

MG 4749

Specimen MG 4749, first referenced by Veiga Ferreira (1958) and historically identified as *S. uniter*, is the most complete snout fragment in the Portuguese fossil record. Both descriptions made for this specimen are in agreement that it is composed of an upper and lower jaw, with a visible row of teeth. However, the historical description posits that the upper jaw is smaller, while the lower jaw is broader. This goes against what is shown in several works (Sollas, 1918; Camp, 1942; Arkhangelsky, 1997; Marek *et al*, 2015), according to which, the upper jaw of an ichthyosaur is generally larger than the lower jaw. With this consideration, it is likely that this is also the case for MG 4749, with the upper jaw actually being the broader one, and what was considered the nasal being the splenial or surangular bone instead (Figure 4.1.1).

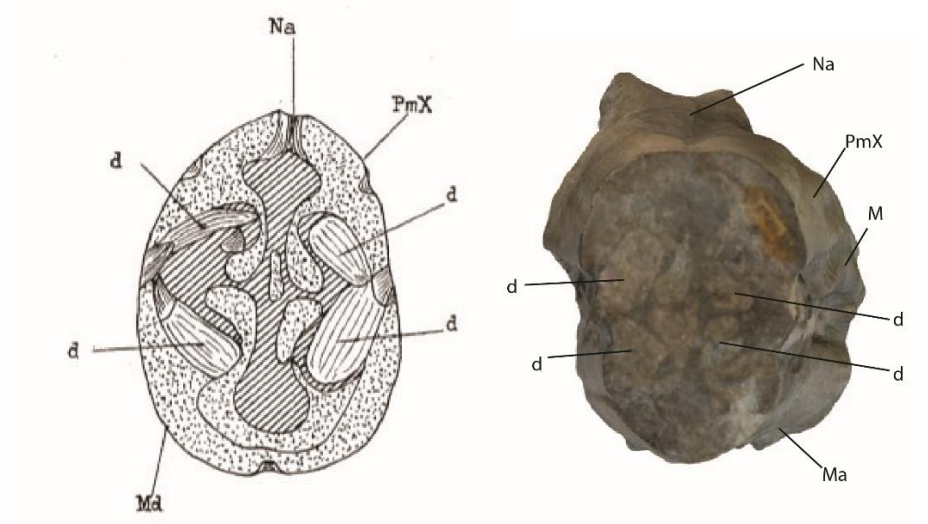

Figure 4.1.1: Comparison between illustration by Veiga Ferreira, 1958, and photogrammetry model. Na-Nasal; PmX-Premaxilla; M-Maxilla; Ma-Lower jaw; d-teeth.

Classifications

Historically, the specimens were classified as either *Stenopterygius* or *Ichthyosaurus*, and in the cases were a species could be determined, as either *S. uniter* or *I. intermedius*, and these classifications match both the age of the specimens and the knowledge available at the time. However, over half a century has passed since, and in that time, the knowledge of ichthyosaur phylogeny has changed significantly. The species *I. intermedius* was described by Conybeare in 1822, although its holotype location is unknown and what figures of it are available are not considered valid. The species was identified largely through tooth morphology, which nowadays is considered highly variable between individuals and thus not a valid character for species identification, and recent work posits that the species is a synonym to *I. communis* (Massare *et al*, 2017). And Stenopterygius taxonomy has varied greatly (Figure 4.2.1). *S. uniter* was recognized as a species by Von Huene in 1931, alongside *S. quadriscissus, S. megacephalus, S. megalorhinus, S. crassicostatus, S. hauffianus, S. banzensis, S. uniter, S. eos, S. incessa, S. longifrons and S. promegacephalus* based on body proportions and vertebral counts, and the classification of Veiga Ferreira (1958) was presumably done under this scheme, but later works by Mcgowan and Godefroit removed *S.uniter* from the taxonomy, and it would not be until the revision of his own work by Maisch in 2008 that is would be recognized as a species once more, although it is not the same as the old classification and is instead considered a new species, from characters previously associated with *S. megalorhinus* and *S. longifrons.*(Maxwell, 2012). Based on this, it can be safely stated that the historical classifications of the Portuguese specimens are outdated.

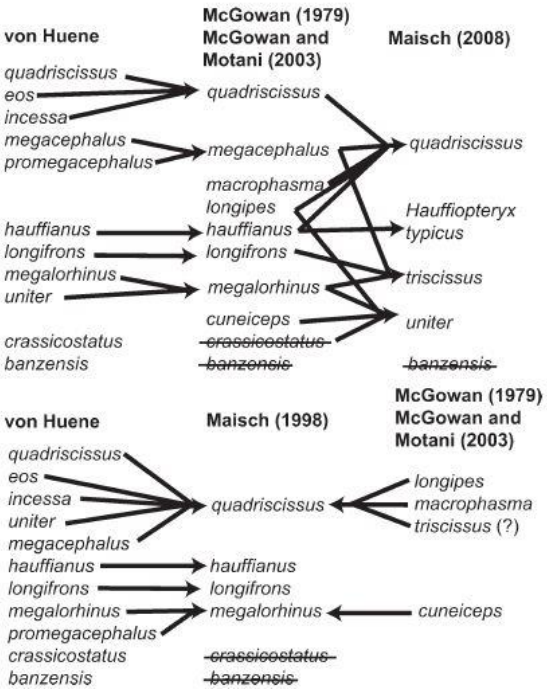

Figure 4.2.1: Diagram depicting the changes in nomenclature of *Stenopterygius* species, from Maxwell, 2012.

Phylogenetic analysis

The results of the phylogenetic analysis performed offer little insight into the possible taxa affinities of the specimens. Due to a low number of observable characters, a vast majority of the specimens are very poorly resolved, being placed in several different locations in the phylogenetic tree simultaneously (See Appendix III). Notably however, the tree itself is also poorly resolved, with 4 large polytomies, and the individual placements of different taxa varying between analyses, which is indicates that some taxa present in matrix may be incompletely or incorrectly classified (Moon, 2017). Of 20 analysed specimens, only one was well resolved and identified as belonging to a species.

Ichthyosaurus larkini

Ichthyosauria de Blainville, 1835

Ichthyosauridae Bonaparte, 1841

Ichthyosaurus De la Beche & Conybeare, 1821

Ichthyosaurus larkini Lomax & Massare, 2016

Described by Lomax and Massare in 2016 mainly through the morphology of the skull and post-cranium, *I. larkini* is the most recent species to be identified in the *Ichthyosaurus* genus. Specimen MDT-IST 85 was unambiguously identified as belonging to the *I. larkini* species. The humerus that lacks a differentiated and offset proximal head (character 198), a plate-like dorsal ridge (character 207), tuberosity at the anterodistal extremity (character 212), anterodistal and posterodistal facets for the sesamoid (characters 213 and 214) or contact with the intermedium (character 215), while sporting a concave anterior margin (character 199), a proximally reduced anterior flange (characters 200 and 201), terminally placed distal facets (character 208), the flattened and plate-like shape of the epipodial and metapodial elements (character 216), an equally sized radius and ulna lacking an interosseous space (characters 220 and 221), the radius being wider than long (character 222), the intermedium (character 228) smaller than the ulnare (character 229) and located between the between the radius and ulna (character 230), the ulnare with a single distal facet (character 236), the large amount of phalanges in each digit (character 249), with the proximal ones being tightly packed polygons (character 250) and the distal ones rounded (character 251), and the presence of digital bifurcation (character 252) are all diagnostic characters of the species that were observed

in the specimen. Notably, specimens MDT-IST 104 and MG 4749, while more poorly resolved, were also placed in this species.

However, one problem remains in this identification. While these 3 specimens range in age from the Sinemurian to the Pliensbachien, the *I. larkini* specimens through which the species was identified are older, from the Hettangian period. While it is not impossible for the species to have existed between these 2 timeframes, this leaves the results of the analyses of Specimens MDT-IST 85, MDT-IST 104, and MG 4749 in doubt.

CONCLUSION

In sum, we conclude that, at the current state of ichthyosaur knowledge:

- The Portuguese ichthyosaur fossil record includes 23 documented fossil occurrences from 8 different localities, with geological units ranging from the Sinemurian (Coimbra formation) to the Aalenian (S. Gião formation), located within the Lusitanian basin.
- Previous work by Sauvage, 1898, Zbyszewski and Moitinho de Almeida, 1952, and Ferreira, 1958, has identified these occurrences as *I. intermedius* and *S. uniter*, but the classifications may be outdated.
- The specimens were re-observed, and new descriptions were made, after which phylogenetic analyses were performed to determine species classification.
- The analyses yielded mostly inconclusive results. Specimen MDT-IST 85 was identified as *I. larkini*, but all the other occurrences did not have a single identification, leaving their identity as ichthyosaur indet.
- Further studies and new developments in ichthyosaur phylogeny are required for a more accurate identification of the Portuguese ichthyosaur specimens. Recent, undocumented discoveries in Alvaiázere and Água de Madeiros may provide important information on the matter.

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Appendix I:

SINAPOMORPHIES (as defined by Benjamin C. Moon, 2017)

Characters of skull

Snout:

1- Extremely slender premaxillary segment, < ¼ the maximum lateral width of the posterior of the skull absent (0) present (1).

Premaxilla:

2- Supranarial process present (0) absent (1).

3- Supranarial process large, extending > 1/3 of the external narial length (0) small, extending < 1/3 of the external narial length (1).

4- Subnarial process absent (0) present (1).

5- Subnarial process small, extending < 1/3 of the external narial length (0) large, extending > 1/3 of the external narial length (1).

Premaxilla-palatine:

6- Contact in central view absent (0) present, relatively broad (1).

Maxilla:

7- Reduction absent, ≥ ½ of the length of the snout (0) present, < ½ of the length of the snout.

8- Teeth present (0) absent (1).

9- Location of the laterally exposed greatest dorsoventral extent posterior to the external naris (0) ventral or anterior to the external naris (1).

10- Length of the premaxillary process short, extends approximately one or less narial lengths anterior to the external naris (0) long, extends approximately 1.5 or more narial lengths anterior to the external naris.

11-Postnarial process exposed laterally (0) not exposed (1).

12- Size of postnarial process exposure large (0) tiny (1).

13- Size of the jugal process long, extending as far under the orbit as the lachrymal in lateral view (0) short, hidden in lateral view by the jugal (1).

14- Contact with prefrontal absent (0) present (1).

15- Contact with external naris in external lateral view present (0) absent (1).

Nasal:

16- Anteroposterior extent of dorsal exposure in the prenarial rostrum substantial, over 40% (0) reduced, less than 40% (1).

17- Nasal posterior extent reaches back to the orbit (0) reaches distinctly over the orbit (1).

18- Narial shelf anterior to the external naris, bordered medially by the nasosupraorbital ridge absent (0) present (1).

19- Nasal borders external naris (0) excluded from external naris (1).

20- Descending process on the anterior posterior border of the nares absent (0) present (1).

21- Nasal-postfrontal contact absent (0) present (1).

22-Nasal-postfrontal contact small (0) extensive, separating frontals and prefrontals in dorsal view.

23- *Excavatio internasalis* absent (0) present (1).

Lachrymal:

24- Anterior extent reaches external naris (0) is excluded from the external naris by the dorsal process of the maxilla and/or the ventral process of the nasal (1).

25- Numerous small-to-medium-sized nutritive foramina absent (0) present (1).

External nares:

26- Shape small, round to ovate (0) elongate (1) elongate and complexly lobate (2).

27- Orientation dorsolateral (0) lateral, scarcely visible in dorsal view (1).

Jugal:

28- Shape triradiate (0) lunate or j-shaped (2).

29- Anterior margin shape tapering, running between the lachrymal and the maxilla (0) broad and fanlike, covering a large area of the maxilla ventrolaterally (1).

30- Extent of the anterior margin terminates posterior to the anterior end of the lachrymal (0) reaches or surpasses the anterior end of the lachrymal.

31- Dorsal ramus shape well-developed and strongly curved dorsally (0) poorly developed, jugal essentially straight (1).

32- Contact between the postorbital process and squamosal absent (0) present (1).

Jugal-quadratojugal:

33- External contact absent (0) present (1).

34- Jugal-quadratojugal notch- deep, forming a pronounced ventral emargination of the cheek present (0) absent (1).

Prefrontal:

35- Dorsal exposure broad (0) present but limited by the anterior process of the postfrontal and posterior process of the nasal (1) little to none (2).

36- Prefrontal-external naris contact absent (0) present (1).

37- Prefrontal-postfrontal contact absent, the dorsal margin of the orbit is formed by the frontal (0) present, eliminating the frontal from the dorsal margin of the orbit (1).

38- Prefrontal and postfrontal high supraorbital crest absent (0) present (1).

Frontal:

39- Dorsal view strongly convex at the anterior edge of the parietal foramen (0) flat to concave, overlapped by surrounding elements (1).

40- Widest exposure located posteriorly (0) at nasal suture (1).

41- Temporal process absent (09 present (1).

42- Frontal does not participates in the supratemporal fenestra in dorsal view (0) participates (1).

43- Size of participation in the supratemporal fenestra small (0) extensive (1).

44- Frontal as large or larger than the parietal (0) frontal smaller than the parietal (1).

Parietal:

45- Dorsal view contribution to the anterior margin of the supratemporal fenestra absent (0) minor (1) large, almost completely excluding the postfrontal from contact (2).

46- Parietal ridge absent (0) present (1).

47- Occipital flange in posterior view present (0) absent (1)

48- Occipital flange large (0) reduced (1).

Parietals:

49- Separation of anterior processes of the right and left narrow, forming a parietal fork and frontal dorsally visible along the pineal foramen (0) widely open, resulting in absence of clear fork (1).

50- Contact between the anterior processes of the right and left present, eliminating the frontal from the parietal foramen (0) absent (1).

51- Anterior fork elevated: absent (0) present (1).

52- Postparietals- Additional bone separating the parietal and supratemporal absent (0) present (1).

53- Size of the Supratemporal process short (0) long (1).

54- Parietal foramen- anteroposterior position approximately equal to the anterior edge of the supratemporal fenestra (0) well anterior to the anterior edge of the supratemporal fenestra.

Postfrontal:

55- Size od the anterior flange delicate and narrow, not extending ventrally to the posterior orbital rim (0) robust and triangular, approaching posterior orbital rim.

56- Size of postfrontal-postorbital contact narrow (0) broad (1).

57- Postfrontal-supratemporal contact absent (0) present (1).

Postorbital:

58- Shape triradiate (0) lunate, without posterior process (1).

59- Broad (0) narrow (1).

60- Participation in supratemporal fenestra present (0) absent (1).

61- Postorbital-supratemporal contact in external view present (0) absent (1).

Supratemporal:

62- Enlargement small, minimal posterior exposure (0) moderate, forming posterior border of the supratemporal fenestra (1) strongly enlarged, forms significant portion of the posterior and lateral borders to supratemporal fenestra and skull roof (2).

63- Anterodorsal sheer overhanging the supratemporal fenestra absent (0) present (1).

64- Size of the descending ramus pronounced, reaching at least half of the total height of the quadrate (0) reduced, a small process medial to the quadrate articulation.

65- Supratemporal-stapes contact absent (0) present (1).

66- Sagittal eminence present (0) absent (1).

67- Postparietal shelf absent (0) present (1).

68- Postparietal shelf small and oblique (0) large and horizontal (1).

Squamosal:

69- Present (0) absent (1).

70- Triangular (0) squared (1).

71- Posterior descending process absent (0) present (1).

72- Participates in supratemporal fenestra (0) excluded by supratemporal and/or postfrontal (1).

73- Posterior half of supratemporal fenestrae in dorsal aspect narrower than anterior half (0) anterior and posterior halves approximately equal in width (1).

74- Anterior terrace of the supratemporal fenestra absent (0) present (1).

75- Anterior terrace of the supratemporal fenestra small, reaching the posterior part of the frontal anteriorly (0) large, reaching the nasal anteriorly (1).

Skull roof:

76- Posterior margin indent in dorsal view deep (0) moderate (1)

Quadratojugal:

77- Main body located laterally (0) posteriorly (1).

78- Exposure broad in lateral view (0) narrow and most extensively expose in posterior view (1).

79- Shape of the ventral edge concave (0) ventral edge straight or entirely covered by the jugal (1).

80- Distinctly offset quadrate process present (0) absent (1).

Quadrate:

81- Dorsal articulation enclosed laterally by the squamosal (0) articulates dorsomedially with the supratemporal only (1).

82- Stapedial facet on the posterior surface ventral half (0) dorsal half (1).

Orbit:

83- Anterior margin irregular (0) regularly rounded (1) angled (2).

Postorbital skull:

84- Length compared to orbital diameter > 1/3 (0) < 1/3 (1).

Cheek:

85- Mostly lateral (0) largely posterior (1).

Interpterygoidal vacuity:

86- Present (0) absent (1).

Palatine:

87- Contributes to subtemporal fenestra posteriorly forming anterior edge (0) posteriorly excluded from the subtemporal fenestra.

Pterygoid:

88- Transverse flange well-developed (0) poorly developed (1)

89- Transverse flange anterolateral (0) posterolateral (1).

90- Posteromedial process present (0) absent (1).

Vomer:

91- One dorsal process (0) two (1).

Epipterygoid ossified:

92- Present (0) absent (1).

Basis cranii:

93- Largely formed by the parasphenoid (0) basisphenoid (1).

Basioccipital:

94- Condyle flat or slightly concave (0) hemispherical (1).

95- Notochordal pit on the condylar surface absent (0) present (1).

96- Notochordal pit on the condylar surface central (0) dorsal (1).

97- Basioccipital peg present (0) absent (1).

98- Prominent ventral tubers separated by a deep notch present (0) absent (1).

99- Extracondylar area present (0) absent (1).

100- Ventral Extracondylar area larger than the dorsoventral height of the condyle (0) smaller than the condyle but still extensive (1) reduced to a thin strip (2).

101- Contribution to the floor of the *foramen magnum* absent, excluded by the exoccipitals (0) present, the portion contributing being flat, or concave, and covered in finished bone (1).

Basisphenoid:

102- Basipterygoidal processes short, giving the basipterygoid a square outline in dorsal view (0) markedly expanded laterally, being wing-like, giving the basisphenoid a marked pentagonal shape in dorsal view (1).

Carotid foramen:

103- Paired (0) unpaired (1).

104- Located in the parasphenoid (0) basisphenoid (1).

Parasphenoid:

105- Shape of the base of the cultriform process wide, gently grading into the basal plate (0) distinctly narrowed, well offset from the basal plate (1).

Parabasisphenoid:

106- Shape in ventral view gradually narrowing posterior to the basipterygoid processes (0) rapidly tapering posteriorly (1).

107- Carotid foramen/foramina located on the ventral surface (0) posterior surface (1).

Opisthotic:

108- Shape of the paraoccipital process short and robust (0) elongate and slender (1).

Supraoccipital:

109- Orientation of the exoccipital processes parallel (0) divergent (1).

Exoccipital:

110- Exoccipitals make the largest lateral contribution to the *foramen magnus* (0) Supraoccipital contribution is almost equal to the exoccipitals (1).

Stapes:

111- Proximal head slender, much smaller than opisthotic proximal head (0) massive, as large or larger than opisthotic.

112- Lateral head less robust than medial head (0) both lateral and medial heads robust (1).

113- Shaft in adults thick (0) slender and gracile (1).

Lower jaw:

114- Well developed (0) reduced (1).

115- Development normal (0) slender, reduced in diameter (1).

116- Ventral margin in lateral view straight or nearly so (0) markedly concave approximately ventral to the external naris (1).

Dentary:

117- Labial shelf present (0) absent (1).

Surangular:

118- Forms most of the posterior lateral surface of the lower jaw, absent (0) present (1).

119- Dorsal (paracoronoid) process just anterior to the jaw articulations absent (0) present (1).

Angular:

120- Anterior lateral exposure much smaller than surangular exposure (0) extensive, at least as high and anteriorly as the surangular exposure (1).

121- Posterior lateral exposure minimal, covers less than half of the lateral surface of the retroarticular process (0) extensive, surangular exposure reduced to a thin strip on the lateral surface of the retroarticular process (1).

Splenial:

122- Participation in the mandibular symphysis more extensive than the dentary (0) present but restricted to the posterior half (1).

Coronoid:

123- Ossified, present (0) absent (1).

124- Laterally flattened (0) narrow and elongate (1).

125- Process flat (0) elevated (1) drawn into a pointed process (2).

Lower jaw glenoid:

126- Deeply excavated, absent (0) present (1).

Articular:

127- Transversally wide with dorsally deeply concave retroarticular process (0) narrow (1).

Teeth:

128- Present (0) absent (1).

Dentition:

129- Complete and well-developed in adults (0) strongly reduced (1).

130- Tooth implantation subthecodont (0) thecodont (1) aulacodont (2).

131- Bony fixation present (0) absent (1).

132- Plicidentine absent (0) present (1).

133- One row of teeth (0) two (1) irregular pavement (2).

134- Upper dental groove present (0) absent (1).

135- Upper dental groove located throughout the jaw margin (0) only anteriorly (1).

136- Lower dental groove present (1) absent (0).

137- Lower dental groove located throughout jaw margin (0) only anteriorly (1).

138- Less than three maxillary positions ventral to the jugal (0) four or more (1).

139- Palatine teeth present (0) absent (1).

140- Pterygoidal teeth present (09 absent (1).

141- Dentition replacement irregular (0) regular (1).

142- Replacement tooth outside the pulp cavity of the predecessor (0) inside (1).

143- Enamel ornamented with prominent ridges and grooves (0) thin and smooth (1) thick and bumpy (2).

144- Root cross-section in adults rounded (0) quadrangular (1).

145- Striations on the root present (0) absent (1).

146- Root striation definition clear (0) subtle (1).

147- Base of the enamel layer poorly defined or invisible (0) well defined and precise (1).

148- Horizontal section of tooth crown circular (0) mediodistally compressed (1) laterally compressed (2).

149- Posterior tooth crown conical (0) rounded (1) flat (2).

Characters of axial skeleton

Atlas:

150- Pleurocentrum anteriorly convex (0) deeply concave (1).

151- Atlas-axis separate (0) co-ossified in adults (1).

152- Neural spines completely overlapping, may be fused (0) functionally separate, never fused (1).

Presacral vertebrae:

153- Number < 30 (0) 30 ≤ number < 55 (1) Number ≤ 55.

Central facets:

154- Bulging (0) central face straight-sided (1).

Cervical vertebrae:

155- Diapophysis-neural arch contact extant up to middle dorsal region (0) anterior dorsal region (1).

156- Height from centrum to neural arch < 2 (0) ≤ 2 (1).

Cervical centra:

157- Bicipital rib facet absent (0) present (1).

Postcervical central:

158- Number of rib articulations holocephalous throughout (0) dicephalous in posterior dorsal and anterior caudal region, remainder holocephalous (1) dicephalous throughout (2).

Dorsal centra:

159- Increase in height from anterior to posterior absent (0) present (1).

160- Anterior dorsal neural spine with normal shape (0) narrow, high and straight (1).

161- Anterior dorsal/ thoracic zygapophyses paired (0) bilobate (1) unpaired (2).

Anterodorsal centra:

162- Rib facet confluent with anterior face in at least some centra (0) not confluent in any (1).

163- Synapophysis symmetrical, hourglass-shaped (0) asymmetrical with irregular swellings and constrictions.

Posterior dorsal centra:

164- Outline ≤ 3.5x high as long (0) ≤ 4x high as long (1).

Sacrum:

165- Present (0) absent, no firm attachment of pelvic girdle by suture by sacral ribs and ilium (1).

166- Two distinguishable sacral ribs (0) undistinguishable (1).

Tail:

167- Longer than precaudal body (0) shorter (1).

168- Lunate tail fin absent (0) present, well developed (1).

169- Caudal peak absent (0) present (1).

Caudal centra:

170- Mid-region height gradually decreasing (0) increasing (1) suddenly decreasing (2).

171- Elongate (0) short (1).

Anterior caudal vertebra:

172- Neural arch to centrum height <2 (0) ≤ 2 (1).

Anterior to middle caudal vertebra:

173- Spinous process very long and slender (0) short and wide (1).

Middle caudal centra:

174- Neural spine inclination distinctly anterior (0) vertical or posterior (1).

Tail fin centra:

175- Strongly laterally compressed (0) as wide as high (1).

Haemapophyses:

176- Ossified, present (0) absent (1).

Chevrons:

177- Present in apical region (0) absent (1).

Ribs:

178- Cross-sectional shape at mid-shaft oval or with posterior groove (0) figure-of-eight (1) round (2) with anterior and posterior flanges (3).

Gastralia:

179- Present (0) absent (1).

180- V-shaped element and arrangement present with one lateral element per side (0) present with two lateral elements (1).

Characters of appendicular skeleton:

Interclavicle:

181- Cruciform (0) triangular (1) T-shaped (1).

Clavicle:

182- Expanded medial flange present (0) absent, clavicle slender and narrow medially (1).

Coracoid:

183- Mediolaterally wider than anteroposteriorly long (0) approximately equidimensional (1) anteroposteriorly longer than mediolaterally wide (2).

184- Medial margin well-rounded (0) straight symphysis (1).

185- Anterior notch present (0) absent (1).

186- Posterior notch present (0) absent (1).

187- Anterior extension longer than posterior (0) reduced anterior extension (1).

188- Anteromedial process present (0) absent (1).

189- Glenoid and scapular facet very small (0) enlarged (1).

190- Medial facet for the scapula absent (0) present (1).

Scapula:

191- Prominent acromion process present (0) absent (1).

192- Anterior expansion proximally *in lieu* of acromion process present (0) absent (1).

193- Anterodorsal margin fan-shaped (0) emarginated (1) straight (2).

194- Glenoid contribution at least as large as the coracoid facet (0) markedly smaller than the coracoid facet (1).

195- Posterior process distinct and large (0) reduced (1).

196- Blade shaft absent (0) present at least proximally (1).

197- Angle subtended by the axis and the glenoid facet nearly parallel (0) 60º or more (1).

Humerus:

198- Differentiated and offset proximal head present (0) absent (1).

199- Anterior margin straight, convex (0) with small central notch (1) markedly concave (2).

200- Anterior flange absent (0) present (1).

201- Anterior flange large, complete (0) reduced proximally (1).

202- Relative width exclusive of anterior flange much proximodistally longer than anteroposteriorly wide (0) approximately equidimensional (1).

203- Dorsal trochanter incipient or none (0) well-developed (1).

204- Protruding deltopectoral crest absent (0) present (1).

205- Development of deltopectoral crest normal (0) large, matching the dorsal trochanter in height, and bordered by concave areas (1).

206- Relative anteroposterior width in dorsal view, excluding dorsal and ventral processes, distal end wider than proximal (0) approximately equal or proximal end wider than distal (1).

207- Plate-like dorsal ridge absent (0) present (1).

208- Position of distal facets not terminal (0) terminal (1).

209- Radial facet larger than ulnar facet (0) radial and ulnar facets approximately the same size (1).

210- Separation of radial and ulnar facets continuous (0) separated by notch (1).

211- Ulnar facet deflected posterodistally, distal facing radial facet absent (0) present (1).

212- Tuberosity at the anterodistal extremity present (0) absent (1).

213- Anterodistal facet for sesamoid absent (0) present (1).

214- Posterodistal facet for sesamoid absent (0) present (1).

215- Intermedium contact absent (0) present (1).

Forelimb:

216- Epipodial and metapodial shape flattened and plate-like (0) strongly thickened (1).

217- Notching of anterior face on leading edge elements (in adults) present (0) absent (1).

218- Notching of posterior face on trailing edge elements (in adults) absent (0) present (1).

219- No postaxial 'complete' accessory digits (0) one (1) two or more (2).

Epipodials:

220- Radius/tibia much larger than ulna/fibula (0) equal in size (1).

221- Interosseous space between Radius and ulna present (0) small foramen (1) absent (2).

Radius:

222- Proximodistal length to anteroposterior width longer than wide (0) wider than long (1).

Ulna:

223- Posterior margin concave (0) notched (1) straight or convex (2).

224- Anteroposterior width, proximal end narrower than distal (0) about equal widths (1).

225- Posterior surface rounded or straight and nearly as thick as the rest of the element (0) concave with a thin, blade-like margin (1).

Manual pisiform:

226- present (0) absent (1).

227- Manual pisiform 2 (neomorph) absent (0) present (1).

Intermedium:

228- Present (0) absent (1).

229- Intermedium smaller than ulnar (0) larger (1).

230- Intermedium distal to the ulna (0) between radius and ulna (1).

231- As wide or wider than long (0) longer than wide (1).

232- Proximal shape straight or notched (0) pointed (1).

233- Distal edge angular (0) flattened (1).

234- One digit directly supported (0) two (1) three (2).

235- Distal facets subequal (0) one much larger than the other(s) (1).

Ulnare:

236- One distal facet, primarily supporting a single digit (0) two, with a posteriorly oriented facet for articulation with metacarpal V (1).

Distal carpals:

237- Five (0) four (1) three (2) two (3).

238- Distal carpal 1 much smaller than metacarpal V (0) similar size or larger (1).

239- Distal carpals 2-3 much smaller than distal carpal 5 (0) of comparable size (1).

240- Distal carpal 4 much smaller than metacarpal V (0) smaller (1).

Manual digits:

241- Four or fewer ossified elements in the metacarpal row (0) five or more (1).

242- Manual preaxial accessory digit absent (0) present (1).

243- Manual digit V with no reduction (0) reduced to small floating element (1).

244- Manual metacarpal I present (0) absent (1).

245- Manual metacarpal I elongate (0) semilunate or rounded (1).

246- Manual metacarpals II-IV shaped like elongate cylinders (0) rounded (1).

247- Manual metacarpal V present (0) absent (1).

248- Posterior margin of manual metacarpal V convex (0) straight or concave (1).

249- Maximum of five or less manual phalanges in a single digit (0) six or more (1).

250- Proximal manual phalanges elongate or hourglass-shaped (0) mostly rounded (1) tightly packed rectangles/polygons (2).

251- Distal manual phalanges elongate (0) rounded (1).

252- Manual digital bifurcation absent (0) present in at least some individuals (1).

Pelvic girdle:

253- Normal-sized (0) moderately reduced (1) strongly reduced (2).

Ilium:

254- Blade with thick shaft (0) plate-like (1) narrow and styloidal (2).

255- Anteromedial prominence present (0) absent (1).

Ischium-pubis:

256- Medial fusion absent (0) present (1).

257- Lateral fusion absent (0) present (1).

258- Ischium and pubis meet medially in well-defined symphysis (0) strongly convex medial margins (1).

259- Pubis larger than ischium (0) similar size or ischium larger (1).

Ischium:

260- Ischium or ischiopubis plate-like, flattened (0) rod-like (1).

261- Great medial edge expansion (0) little or none (1).

262- Acetabular contribution greater than pubis (0) subequal with pubis (1).

Pubis:

263- Obturator foramen present (0) absent (1).

264- Obturator foramen completely enclosed in pubis (0) mostly in pubis but open on one side (1) part of obturator fossa (2).

265- Distance between the obturator foramen(/incision) and the distal margin large (0) small (1).

Femur:

266- Relative proximodistal length to anteroposterior width much longer than wide (>2x) (0) shorter and wider, with distinct medial constriction (1).

267- Prominent, ridge-like dorsal and ventral processes demarcated from the head and extending up to mid-shaft absent (0) present (1).

268- Ventral process smaller than dorsal process (0) same size or larger, more prominent (1).

269- Wide distal blade present (0) absent, subequal proximal and distal widths (1).

270- Anterodistal facet for anterior accessory epipodial element anterior to the tibia absent (0) present (1).

271- Tibial facet size larger than fibular facet (0) subequal (1).

Tibia:

272- Proximodistally longer than anteroposteriorly wide (0) wider than long (1).

273- Anterior margin concave (0) notched (1) straight or convex (2).

274- Posterior margin concave (0) notched (1) straight or convex (2).

275- Proximodistal length approximately twice as long as more distal elements (0) only slightly longer (1).

Tibia and fibula:

276- Tibia larger than fibula (0) approximately equal (1) tibia proximodistally and anteroposteriorly smaller (2).

277- Proximal contact absent (0) present (1).

Fibula:

278- Anterior margin concave (0) notched (1) straight or convex (2).

279- Not fixed, mobile relative to femur (0) much posterior relative to the femur (1) about the same level (2).

Astragalus:

280- Between tibia and fibula (0) distal to tibia (1).

Distal tarsals:

281- Five (0) four (1) three (2).

Pedal digit 1:

282- Present (0) absent (1).

Hindlimb:

283- Notching on anterior of leading edge metapodials absent (0) present (1).

284- Notching on posterior of trailing edge metapodials absent (0) present (1).

285- Pedal post axial accessory digit absent (0) present (1).

Metatarsals:

286- Elongate or hourglass shaped (0) shortened and rounded (1) polygonal (2).

Pedal phalanges:

287- Elongate or hourglass (0) rounded (1) polygonal (2).

Appendix II:

The specimen characters, based on Benjamin C. Moon, 2017.

? represents characters that are uncertain or not observable; - represents characters not present in the specimen.

MG4747

[0-40] -

[41-80] -

[81-120] -

[121-160] -

[161-200] -

[201-240] - - - - - - - - - - - - - - - 0 0 ? ? ? 2 1 ? ? ? ? ? 0 ? 1 0 0 0 ? 1 - - - - -

[241- 287] -

MG37

[0-40] -

[41-80] -

[81-120] -

[121-160] -

[161-200] -

[201-240] -

[241- 287] ? ? ? ? ? ? ? ? 1 1 1 ? -

MG4750

[0-40] - - - - - - - - - - -

[41-80] -

[81-120] -

[121-160] -

[161-200] -

[201-240] -

[241- 287] - 1 ? ? ? 0 1 - - - - - - - - - - - - - - - -

MG4751

[0-40] - ? ? ? ? -

[41-80] -

[81-120] - ? ? ? ? - - -

[121-160] - - - - - - - 0 0 ? ? 0 ? ? ? ? ? ? ? ? ? ? 0 0 0 1 ? 0 ? - - - - - - - - - - -

[161-200] -

[201-240] -

[241- 287] -

MG4755

[0-40] - - - - - - - - - - -

[41-80] - - - - - - - - - -- -

[81-120] -

[121-160] -

[161-200] -

[201-240] -

[241- 287] -

MG4749

[0-40] 0 0 0 1 ? - 1 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? - - - - - - - - - - - - - - - - -

[41-80] - - - - - - - - - -- -

[81-120] - 0 0 1 0 - - -

[121-160] - 1 - - - - - 0 0 2 1 0 0 0 0 0 0 ? 1 1 0 1 0 0 0 1 1 0 0 - - - - - - - - - - -

[161-200] -

[201-240] -

[241- 287] -

MG4743

[0-40] - - - - - - - - - - -

[41-80] - - - - - - - - - -- -

[81-120] -

[121-160] -

[161-200] -

[201-240] -

[241- 287] -

MG36

[0-40] 0 ? ? ? ? -

[41-80] - - - - - - - - - -- -

[81-120] - 0 0 1 0 - - -

[121-160] - - - - - - - 0 0 2 ? 10 0 0 0 0 ? 1 1 0 ? 0 0 0 1 ? 0 ? - - - - - - - - - - -

[161-200] -

[201-240] -

[241- 287] -

MG25186

[0-40] - - - - - - - - - - - -

[41-80] - - - - - - - - - - --- -

[81-120] -

[121-160] - ? ?

[161-200] ? ? ? ? - - - - - - - - - - - - - - - 0 -

[201-240] -

[241- 287] -

MG25182

[0-40] - - - - - - - - - - - -

[41-80] - - - - - - - - - - --- -

[81-120] -

[121-160] - 0 ?

[161-200] 0 ? ? 0 -

[201-240] -

[241- 287] -

MG25183

[0-40] - - - - - - - - - - - -

[41-80] - - - - - - - - - - --- -

[81-120] -

[121-160] - 0 ?

[161-200] ? ? ? 0 -

[201-240] -

[241- 287] -

MG4753

[0-40] -

[41-80] -

[81-120] -

[121-160] -

[161-200] - - - - - - - - - - ? 1 ? ? 1 -

[201-240] -

[241- 287] -

MDT-IST 85

[0-40] -

[41-80] -

[81-120] -

[121-160] -

[161-200] - 1 2 1

[201-240] 1 0 1 0 - 0 0 1 1 0 0 1 0 0 0 0 1 1 1 1 2 1 2 2 0 1 0 0 0 1 0 1 0 1 ? 0 0 ? 1 ?

[241- 287] 0 0 1 1 - 1 1 - 1 2 1 1 -

MDT-IST 104

[0-40] -

[41-80] -

[81-120] - ? ? ? ? - - -

[121-160] - - - - - - - 0 0 ? 1 ? 0 ? ? ? ? ? ? ? ? 0 0 0 1 1 0 ? - - - - - - - - - - -

[161-200] -

[201-240] -

[241- 287] -

MDT-IST 103

[0-40] -

[41-80] -

[81-120] -

[121-160] - ? ?

[161-200] ? ? ? 0 -

[201-240] -

[241- 287] -

MG4745

[0-40] -

[41-80] -

[81-120] -

[121-160] -

[161-200] - - - - - - - - - ? 1 - - 1 1 -

[201-240] -

[241- 287] -

MG4748

[0-40] -

[41-80] -

[81-120] -

[121-160] -

[161-200] - - - - - - - - - ? 1 ? ? ? 1 -

[201-240] -

[241- 287] -

MG4746

[0-40] -

[41-80] -

[81-120] -

[121-160] -

[161-200] - - - - - - - - - ? 1 ? ? ? 1 -

[201-240] -

[241- 287] -

MG25184

[0-40] -

[41-80] -

[81-120] -

[121-160] -

[161-200] - - - - - - - - - ? 1 ? ? ? 1 -

[201-240] -

[241- 287] -

MG4752

[0-40] -

[41-80] -

[81-120] -

[121-160] -

[161-200] - - - - - - - - - ? 1 2 1 1 1 -

[201-240] -

[241- 287] -

MG35

[0-40] -

[41-80] -

[81-120] -

[121-160] - - - - - - - 0 0 ? ? ? 0 ? ? ? ? ? 1 ? 0 ? 0 0 0 0 0 0 0 - - - - - - - - - - -

[161-200] -

[201-240] -

[241- 287] -

Appendix III

Specimen photogrammetry models

MG 4749: Max quality of faces-4.8M; Error margin-16µm.

Left view

Right view

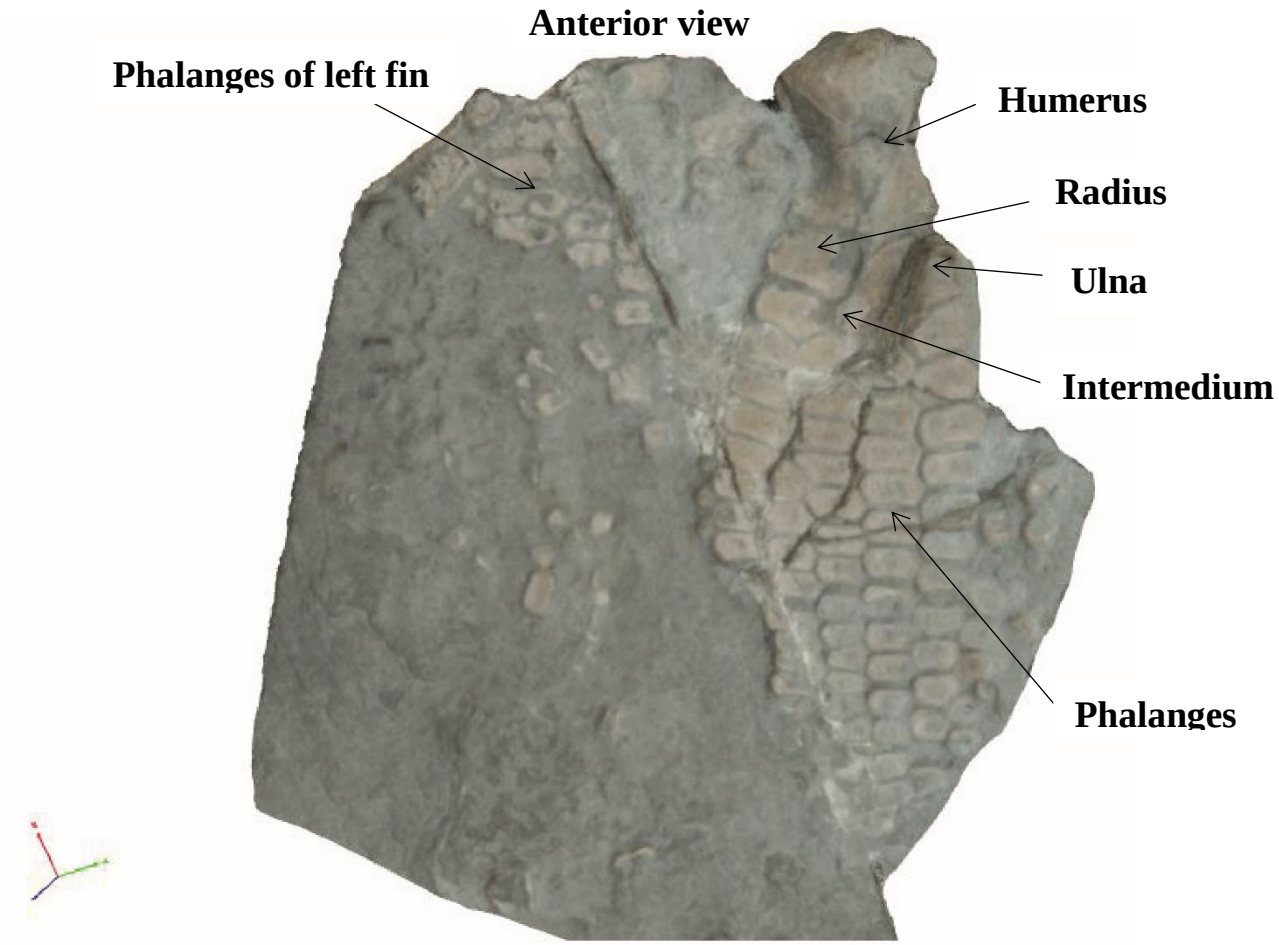
Anterior view

Posterior view

Dorsal view

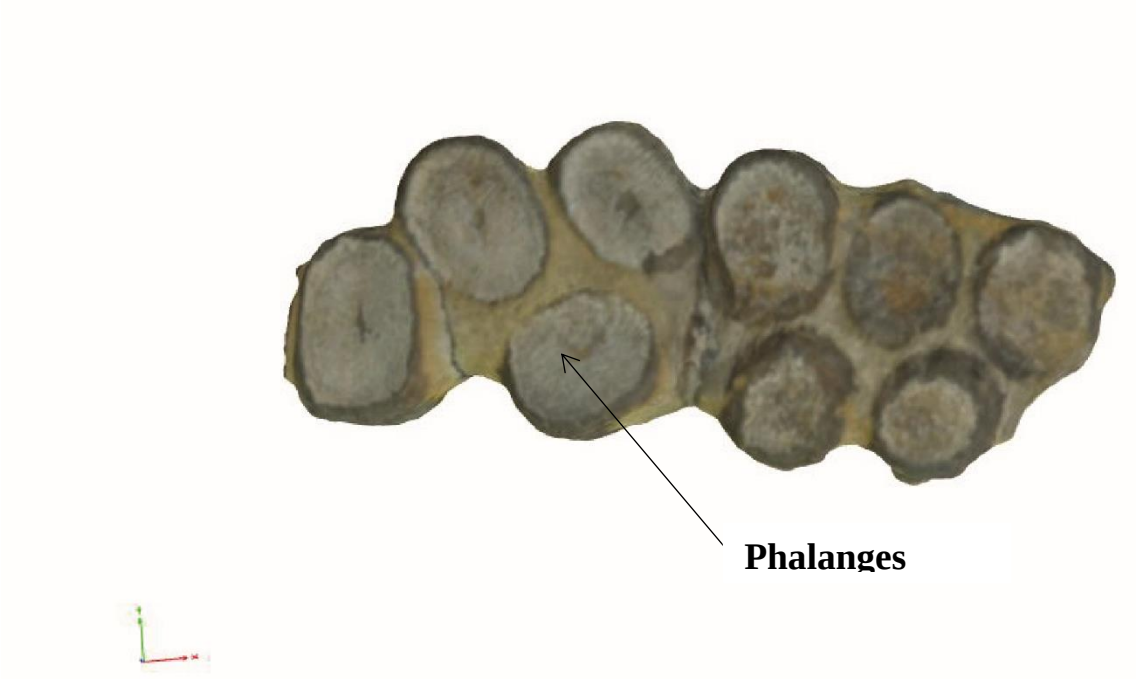
Ventral view

85: Max quality of faces-13.6M; Error margin-9µm.



MG 4747: Max quality of faces-2.9M; Error margin-10µm.

MG 37: Max quality of faces-0.8M; Error margin-9µm.



MG 4750: Max quality of faces-1.8M; Error margin-11µm.

Dorsal view

Ventral view

Left view

Right view

Anterior view

Posterior view

MG 36: Max quality of faces-2.2M; Error margin-19µm.

Right view

Left view

Anterior view

Posterior view

Dorsal view

Ventral view